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Zoogeography of Peruvian Bats With Special Emphasis on the Role of the Andes

KARL F. KOOPMAN¹

ABSTRACT

The known distribution of each of 122 species of bats from Peru is summarized. The Andean mountain chain affects these distributions both as a barrier and as a creator of habitat differentiation. Three main distributional areas are distinguished, the humid Amazonian lowlands (below 1000 m.), the highlands within the Amazonian drainage (above 1000 m.), and the chiefly arid Pacific slopes. Some

complications occur in northwestern Peru, where the Pacific slopes (particularly the higher portions) are not arid, there are a few relatively low passes across the Andes, and the upper portions of certain Amazonian tributaries are arid. Instances of ecological (including altitudinal) replacement and specific or subspecific representation between the major ecological zones are discussed.

INTRODUCTION

The American Museum of Natural History received a large number of bats from three altitudinal transects in Peru, collected by John Terborgh and John S. Weske, which has prompted a reexamination of the systematics and distribution of Peruvian bats with particular attention to altitude. Since Tuttle (1970) has published a very useful account on the same general subject, this paper emphasizes additions to and, in a few cases corrections of, Tuttle's information. In many cases, Tuttle gave only marginal records, whereas I include additional records. My report, in general, is based on specimens in the American Museum of Natural History, including the Terborgh-Weske collection, part of the material reported by Tuttle, and earlier material, chiefly collected by Olalla, Schunke, Bassler, and Watkins. Some speci-

mens in other museums have been studied, however, and are referred to when they yield additional information.

The Terborgh-Weske bats were preserved in formalin. Because they were collected entirely by netting, some groups (e.g., Glossophaginae, Carollinae, Stenoderminae) are very well represented, some are poorly represented, and some (e.g., Emballonuridae, Molossidae) are not represented. The main emphasis is on phyllostomatid bats. Altitudinal data for the poorly represented groups are scanty. While there is an extensive literature on both highland and lowland Peruvian bats, much of it gives no data on altitude. For the purposes of this paper, lowland is below 1000 m., highland is above 1000 m. Some of the general conclusions have already appeared (Koopman, 1976).

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SYSTEMATIC ACCOUNTS

FAMILY EMBALLONURIDAE

Rhynchonycteris naso (Wied-Neuwied)—This species appears to be restricted to the Amazonian lowlands. Tuttle (1970) recorded it from the departments of Loreto, Pasco, and Cuzco. The American Museum also has specimens from Amazonas (mouth of the Cenipa River, AMNH 98757-58).

Saccopteryx bilineata (Temminck)—This is another lowland species. (Tuttle's record from San Ramón at ca. 900 m. may be the highest recorded for Peru.) Tuttle mentioned the departments of Loreto, Pasco, Junín, and Cuzco. The American Museum also has specimens from Huánuco (Montealegre, AMNH 67228-29) and the Field Museum has speci-

mens from Madre de Dios (Inambari River mouth) and Ayacucho (Sivia). All these records are from the Amazonian side, however, the Field Museum has specimens from Tumbes (Matapalo) on the Pacific side.

Saccopteryx canescens Thomas—Tuttle (1970) recorded this species only from Huánuco, though the locality (Puerto Victoria, Rio Pachitea) is in the Department of Pasco according to the maps I've seen. Ceballos Bendezu (1968) recorded the species from Loreto. Presumably it is confined to the Amazonian lowlands. The American Museum has no Peruvian material.

Saccopteryx leptura (Schreber)—The upper altitudinal limit given by Tuttle (taken from Thomas, 1893) is at ca. 900 m. (Chanchamayo, near Tarma, Junín). Tuttle (1970) recorded the species from Loreto, Pasco, and Cuzco, but Ceballos Bendezu (1968) believed the Cuzco locality (Bellavista) to be an error for Buena Vista in the Department of Madre de Dios. The American Museum has a specimen from Amazonas (Pomara, AMNH 69235, unfortunately, no altitude given). The species is probably widespread in the Amazonian lowlands.

Cormura brevirostris (Wagner)—This appears to be an Amazonian lowland species, recorded from Loreto, Huánuco, and Pasco by Tuttle, and from Madre de Dios by Ceballos Bendezu (1968). The few specimens from Peru in the American Museum are all from Loreto. The Huánuco record (Tingo Maria) at ca. 700 m. is probably the highest for Peru.

Peropteryx kappleri Peters—Tuttle recorded this species from Pasco and Cuzco. The Pasco record is in the lowlands, but the Cuzco locality (Hacienda Cadena) is at ca. 1500 m. The American Museum has no Peruvian specimens.

Peropteryx macrotis (Wagner)—Tuttle (1970) recorded this species from the departments of Loreto, Pasco, Cuzco, and Puno. The Field Museum has specimens from Madre de Dios (La Pampa). If the record from Cuzco (Machu Picchu) is accurate, this species is unusual for its family in reaching an altitude of ca. 1850 m., but confirmation of this is desirable. The American Museum material from Peru is all from Loreto except for a Tuttle specimen. The

Texas Cooperative Wildlife Collection has specimens from San Martín and Huánuco.

Peropteryx (Peronymus) leucopterus Peters—This Amazonian lowland species was recorded by Tuttle only from Loreto. The American Museum has no Peruvian material.

Centronycteris maximiliani (Fischer)—I have nothing to add to the single vague locality that Tuttle (1970) gave except to point out that this is otherwise an Amazonian lowland species. The American Museum has no Peruvian specimens.

Diclidurus albus Wied-Neuwied—I have nothing to add to Tuttle's Loreto record based on a single specimen in the American Museum. This is an Amazonian lowland species.

Diclidurus scutatus Peters—Tuttle's single record was based on a specimen without definite locality in the American Museum of Natural History. The species is apparently a lowland Amazonian one.

FAMILY NOCTILIONIDAE

Noctilio albiventris Demarest—I follow Hershkovitz (1975) and Davis (1976) in using this name instead of *N. labialis*. An Amazonian lowland species, it was recorded by Tuttle from Loreto, Pasco, and Cuzco. Davis (1976) recorded it from Huánuco. The American Museum has a specimen from San Martín (Pachiza, Monte Alegre, AMNH 98697).

Noctilio leporinus (Linnaeus)—This lowland species was recorded by Tuttle only from Loreto and Pasco. All American Museum specimens come from these two departments in the Amazonian lowlands, but the Field Museum has a specimen from Tumbes (Huásimo) on the Pacific side.

FAMILY MORMOOPIDAE

Pteronotus parnellii Gray—This Amazonian lowland species is known only from the Department of Huánuco (Tuttle, 1970; Smith, 1972). The American Museum has no Peruvian specimens. The highest known altitude for this species in Peru is at ca. 700 m.

Pteronotus davyi (Gray)—Tuttle did not mention this species but Smith (1972) recorded it from several localities in the departments of

Cajamarca and Piura (including three specimens in the American Museum). These populations are widely separated from the remainder of the range of the species in Costa Rica, Venezuela, and areas farther north and are considered by Smith to form a distinct subspecies (*P. d. incaae*), which occupies both sides of the divide between the Pacific and Amazonian slopes. In this region, as discussed by Tuttle (1970), the divide is at its lowest, and one might expect *P. davyi* to reach altitudes of at least 2100 m. in order to get through these relatively low passes. Unfortunately the only altitudinal data are for the type locality on the Pacific side, which is quite low (ca. 300 m.). The altitude of two localities on the Amazonian side, Jaen (Cajamarca) and Huancabamba (Piura) are each at ca. 2000 m., however, and the species probably does not occur in the Amazonian lowlands.

Pteronotus gymnonotus (Natterer)—I follow Smith (1977) in using this name in place of *suapurensis*. Tuttle (1970) recorded the species only from Loreto, but Smith (1972) recorded it also from Huánuco and Piura. Although Smith stated (p. 104) that the species occurs "west of the Andes in Piura Province," the Piura locality (Huancabamba) is in the Amazonian drainage, near the divide. No altitude was given, but Huancabamba is near 2000 m. The other localities are in the Amazonian lowlands.

FAMILY PHYLLOSTOMATIDAE

Micronycteris behni (Peters)—This poorly known form in Peru is recorded only in Rio Cosnipata. Tuttle stated the locality to be in Puno (but in Cuzco *fide* Vaurie, 1972, p. 13). No altitude was given, but it is probably below 1000 m. The species is known otherwise only from the Brazilian state of Mato Grosso in the eastern lowlands. The American Museum has no specimens.

Micronycteris hirsuta (Peters)—This Amazonian lowland species was recorded by Tuttle only from Pasco. The American Museum has no Peruvian specimens.

Micronycteris megalotis (Gray)—Tuttle (1970) recorded this species from Loreto, Huánuco, Pasco, Junín, and Cuzco. The American Museum has specimens from Piura (Pa-

lambla at ca. 1200 m., AMNH 63722, 63731-33) and the Field Museum from Tumbes (Huásimo), both on the western slope, though not in the arid Pacific lowlands. The occurrence of the species on both sides of the Andes is not surprising in view of the fact that *M. megalotis* goes from the lowlands up to 1700-1800 m. in the Cordillera Vilcabamba of Cuzco (Terborgh-Weske, AMNH 233219) and to 2700 m. near Carpath Pass in Huánuco (Short, AMNH 216102). Pirlot (1968) recorded it from 3400 m. in Junín.

Micronycteris minuta (Gervais)—Tuttle recorded this Amazonian lowland species only from Pasco. The American Museum has specimens from Loreto (Puerto Indiana, AMNH 73495-96, 73498-99; Boca Rio Curaray, AMNH 71614-18, 71621, 71628-31) and Cuzco (Rio Mapitunari, AMNH 233221).

Micronycteris nicefori Sanborn—Tuttle recorded this Amazonian lowland species only from Loreto. The American Museum has no Peruvian specimens.

Micronycteris sylvestris (Thomas)—Tuttle did not record this Amazonian lowland species from Peru, but the American Museum has a specimen from Cuzco (Cordillera Vilcabamba, west side, 890 m., AMNH 214316).

Micronycteris (*Barticonycteris*) *daviesi* (Hill)—This rare Amazonian species was recorded by Tuttle only from Pasco. The American Museum has no specimens. My reasons for considering *Barticonycteris* a subgenus of *Micronycteris* are primarily cladistic. I believe that its characters (enlargement of the inner upper incisors with loss of the small outer upper incisors, procumbency of the lower incisors, premolarization of the upper canines, broadening of the upper premolars) are simply those of *M. (Glyphonycteris)*, the subgenus including *sylvestris* and *behni*, carried one step further.

Lonchorhina aurita Tomes—This rare but widespread species was recorded by Tuttle only from the Amazonian lowlands of Pasco, but the Texas Cooperative Wildlife Collection has specimens from ca. 750 m. in Huánuco. *Lonchorhina a. occidentalis* is still known only from the Pacific side of Ecuador. The American Museum has a second specimen, a to-

potype, collected within a month of the type. The topotype (AMNH 62940) differs from the holotype in lacking pale wing patches but resembles it in skull and noseleaf length. Two of Tuttle's Peruvian specimens have been compared with the two *L. a. occidentalis* and with several specimens of *L. a. aurita* from Trinidad, Venezuela, and Colombia. These Peruvian specimens agree with *L. a. aurita* rather than with *L. a. occidentalis*. They are clearly not *L. orinocensis* as compared with the figures in Linares and Ojasti (1971).

Macrophyllum macrophyllum (Schinz)—Tuttle (1970) recorded this Amazonian lowland species from Loreto, Amazonas, and Pasco. The American Museum has no other Peruvian specimens.

Tonatia brasiliensis (Peters)—Tuttle omitted this species, but Gardner (1976) recorded it from both Loreto and Junín, and the Field Museum has specimens from Cuzco (Huajyumbé). Gardner suggested that *venezuelae*, *minuta*, and *nicaraguae* are all conspecific with it, in which case it is probably a widespread Amazonian lowland species. The only American Museum specimens are Goodwin's (1942) original series of *minuta* from Loreto.

Tonatia carrikeri (J. A. Allen)—Tuttle did not mention this Amazonian lowland species, but Gardner (1976) recorded it from Loreto. The American Museum has no Peruvian specimens.

Tonatia bidens (Spix)—Tuttle and Gardner both recorded this Amazonian lowland species only from Loreto. The American Museum has no other Peruvian specimens.

Tonatia sylvicola (D'Orbigny)—Tuttle recorded this widespread species from Loreto, Huánuco, Pasco, and Cuzco, and the Field Museum has specimens from Madre de Dios and Junín (Chanchamayo), all on the Amazonian slopes. All American Museum Peruvian specimens are from Loreto except for Tuttle's. The record from Hacienda Cadena (Cuzco) at ca. 1500 m. appears to be the highest for the Atlantic slope of Peru. However, the Texas Cooperative Wildlife Collection and the Field Museum have specimens from Piura on the Pacific slope at elevations from ca. 300 m. to ca. 2000 m.

Mimon crenulatum (E. Geoffroy)—Tuttle (1970) recorded this species from Loreto and Pasco, and Thomas (1927a) from San Martín. Handley (1960) also included Huánuco on the basis of a species (*peruana*) which he synonymized with *M. crenulatum longifolium*. Gardner and Patton (1972) described a new species (*M. koepckee*) on the basis of three specimens from two highland (1660-1810 m.) localities in Ayacucho. These were compared with seven specimens of *M. crenulatum* from a single locality in Loreto. The American Museum has a single specimen (AMNH 233222) in the Terborgh-Weske collection from Estera Rohuana (lat. 12°43'S, long. 73°47'W), probably the same as one of Gardner and Patton's localities at 1900 m. in the Department of Ayacucho. It agrees very well with the description and skull photograph of *koepckee* given by Gardner and Patton. This specimen has been compared with 11 Peruvian skulls of *M. c. longifolium* and numerous skulls of *M. crenulatum* from elsewhere in South America, all in the American Museum. Three of the Peruvian skulls were used by Handley (1960) in his study (where the "Boca de Rio Curaray" specimen was erroneously stated to be from Ecuador) and seven are Tuttle's. I have emphasized skulls partly because I consider them more useful, and partly because the external characters given by Gardner and Patton do not distinguish the two alcoholic Peruvian specimens (one *M. c. longifolium*, one *M. koepckee*) which I have had available for comparison. The series of 10 skins from Loreto, Pasco, and Huánuco, however, though they are fairly uniform in general color, show considerable variation in the distinctness of the dorsal stripe. For each of the skull characters used to distinguish *koepckee*—smaller size, more pronounced rostral tapering, lesser rostral inflation and absence of median depression (which are really a single character), lesser degree of auditory bullar inflation, less well-developed lingual cingular cleft—the *koepckee* skull stands at one extreme of the *crenulatum* variation. However, in each of these characters, there is considerable variation within *crenulatum* and usually in *M. c. longifolium* and some individuals are quite close to *koepckee*. To me,

therefore, the relationship is better expressed by regarding *koepckee* as a Peruvian highland subspecies of *M. crenulatum*, of which I therefore recognize two Peruvian subspecies: *M. c. longifolium* of the Amazonian lowlands (known from Loreto, San Martín, Huánuco, and Pasco); *M. c. koepckee* of the highlands (known only from Ayacucho). The formal synonymy of *Mimon crenulatum* would therefore stand as follows:

- Phyllostoma crenulatum* E. Geoffroy, 1810, p. 193.
Type locality, "Brazil."
- Phyllostoma longifolium* Wagner, 1843, p. 365.
Type locality, Villa Maria, Mato Grosso, Brazil.
- Anthorhina picata* Thomas, 1903, p. 659. Type locality, Lamarão, Bahia, Brazil.
- Anthorhina peruana* Thomas, 1923, p. 693. Type locality, Rio Pachitea, Huánuco, Peru.
- Mimon crenulatum keenani* Handley, 1960, p. 463.
Type locality, Fort Gulick, Canal Zone, Panama.
- Mimon koepckee* Gardner and Patton, 1972, p. 7.
Type locality, Huanhuachayo, Ayacucho, Peru.

Phyllostomus discolor Wagner—Tuttle considered the previous record of this species erroneous, but Gardner (1976) recorded it from Loreto and Huánuco. The American Museum has two specimens from Huánuco (Rio Lullapichis, 250 m., AMNH 233223-24) and the Field Museum has specimens from Madre de Dios (Itahuana) in the Amazonian basin and from Piura (Salitral) on the Pacific side. The record from Tingo Maria (ca. 700 m.) is probably the highest for Peru.

Phyllostomus elongatus E. Geoffroy—This Amazonian species was recorded by Tuttle only from Pasco and Cuzco, the latter from as high as 1500 m. (Hacienda Cadena). Specimens collected by Terborgh and Weske in Cuzco are all from 950 m. or lower. The American Museum also has 19 specimens from Loreto and the Field Museum has specimens from Madre de Dios.

Phyllostomus hastatus (Pallas)—Tuttle recorded this species from San Martín, Pasco, and Cuzco. The American Museum has 67 specimens from Loreto, one from Junín (San Ramón, AMNH 213203), and four from Amazonas (Pomara, AMNH 69222-25). The Texas Cooperative Wildlife Collection has specimens

from Huánuco and the Field Museum has specimens from Madre de Dios (Colpa, Rio Tambopata) and Ayacucho (Ayna forests; Candallasa) on the Amazonian side and from Tumbes (Matapalo) on the Pacific. With the possible exception of the San Martín localities, which Tuttle lists, and Pomara (in Amazonas), whose altitudes are unfortunately not given, the highest record for Peru appears to be Ayna forest at ca. 1900 m. in Ayacucho.

Phylloderma stenops Peters-Tuttle (1970) did not mention this species. Although it occurs in the Amazonian lowlands of Brazil and Colombia, the only published Peruvian record (Gardner, 1976) is from ca. 2660 m. in Ayacucho. The American Museum has no Peruvian specimens, but the Texas Cooperative Wildlife Collection has specimens from Loreto in the Amazonian lowlands and Piura on the Pacific slope.

Trachops cirrhosus (Spix)—This Amazonian lowland species was recorded by Tuttle (1970) only from Loreto and Pasco. The American Museum has specimens from Huánuco (Rio Lullapichis, 220-250 m., AMNH 233227, 236002) and the Field Museum from Madre de Dios (Manú).

Vampyrus spectrum (Linnaeus)—Tuttle recorded this rare Amazonian lowland species only from Loreto and Cuzco. The American Museum has no Peruvian specimens.

Glossophaga soricina (Pallas)—Tuttle recorded this widespread species from Loreto, Pasco, Junín, and Cuzco on the Amazonian side and from Tumbes and Arequipa on the Pacific slope. De la Puente (1951) listed Amazonas on the east and Piura, Libertad, Lima, and Ica on the west. The American Museum has specimens from Huánuco (Tournavista, AMNH 214135-39; Cerros del Sira at 1120 m., AMNH 236003) and San Martín (Pachiza, AMNH 98726). The Field Museum has specimens from Madre de Dios on the east and from Lambayeque and Ancash on the west. The Cerros del Sira record is the highest elevation from which Terborgh-Weske collected *Glossophaga*, but one of the Cuzco records (Idma at ca. 1850 m.) is considerably higher. Although the subspecies, in general, on the two sides are different (*G. s. soricina* on the eastern and *G. s.*

valens on the western) it is evident that *G. soricina* comes close to reaching the 2150 m. it needs to cross through the Andean passes of northern Peru (see Tuttle, 1970, p. 54). Actually, the population in the arid upper Marañon Valley (therefore in the Amazonian drainage) is referable to *G. s. valens* of the west rather than to *G. s. soricina* of the east (Miller, 1913).

Lonchophylla hesperia G. M. Allen—This rare endemic Peruvian species was recorded by Tuttle only from Tumbes and Libertad. Gardner (1976) recorded it also from Cajamarca, which extended its range from the arid Pacific coast of Peru to an arid marginal portion of the Amazon drainage. The American Museum has no specimens, but the Texas Cooperative Wildlife Collection has specimens from both Piura on the Pacific side and an arid portion of Amazonas (15 km. WNW Bagua Grande) on the Amazonian side.

Lonchophylla thomasi J. A. Allen-Tuttle (1970) did not mention this Amazonian lowland species, but four specimens in the American Museum received from him (AMNH 230281-84), collected in Pasco (San Juan and San Pablo) are of this species. Gardner (1976) recorded it from Loreto, and explained that the specimen from Loreto that Pirlot (1968) recorded as *concava* and Tuttle as *mordax* is very probably also referable to *L. thomasi*. This is most reasonable in view of the fact that all specimens of small *Lonchophylla* I have seen from the Amazon basin are referable to *L. thomasi*.

Lonchophylla robusta Miller-Tuttle (1970) recorded this Amazonian lowland species only from Pasco and Junín. The Junín locality is at ca. 900 m., the highest known for Peru. Gardner (1976) also recorded it from Junín. The American Museum has no Peruvian specimens except for one of Tuttle's.

Platalina genovensium Thomas-Tuttle recorded this strictly Peruvian species from Piura, Lima, Arequipa, and Huánuco. The first three are on the Pacific slope, the last in a rather isolated semiarid portion of the Amazon basin. Both the Arequipa and the Huánuco localities are at altitudes near 2000 m. It is therefore not surprising that this species has managed to get through relatively low passes of the Andes to

colonize the Amazonian drainage. Presumably its restricted distribution in the latter is due to its adaptation to arid areas. The American Museum has no specimens of this species.

Lionycteris spurrelli Thomas—Tuttle recorded this Amazon basin species from Cuzco (the Quincemil specimen from 2000 ft. in the American Museum) and Pasco. However, of the five Pasco specimens received from him and identified as *Lionycteris*, only one (AMNH 239891), collected at Nevati, actually belongs to this species. The others (from San Juan and San Pablo) are referable to *Lonchophylla thomasi*. The American Museum also has a good series from Huánuco (Cerros del Sira, AMNH 236004-027) at 1120 m. The Texas Co-operative Wildlife Collection has specimens from San Martín.

Anoura brevirostrum Carter—This species, apparently endemic to the Andean region from Colombia to Peru, was recorded by Tuttle only from Huánuco. The localities are all quite low (600-850 m.) on the Amazonian slope. The American Museum has many specimens collected by Terborgh and Weske from Ayacucho (Huanhuachayo, AMNH 233250-55, 233261-69) and Cuzco (Cordillera Vilcabamba, west side, AMNH 214324, 233256-57), also on the Amazonian slopes, but at considerably higher altitudes (1270 to 2260 m.). Gardner's (1976) Huánuco record is only slightly below the highest of these. The distribution is therefore peculiar in including low, as well as high, elevations, but not extending east away from the mountains.

Anoura caudifer (E. Geoffroy)—Tuttle (1970) recorded this species from Junín, Cuzco, and Puno. The American Museum also has specimens from Loreto and Huánuco (22 specimens from Cerros del Sira). All Peruvian localities are on the Amazonian side of the Andes. Tuttle indicated an altitudinal range in Peru of ca. 600-2750 m. The Loreto record (Boca Rio Curaray, AMNH 71624) carries it down to ca. 150 m., while the highest altitude from which Terborgh and Weske obtained this species was at 2825-2845 m. (Cordillera Vilcabamba, west side, AMNH 233270) in Cuzco.

Anoura geoffroyi Gray—Tuttle recorded this species from San Martín, Junín, and Cuzco on

the Amazonian side and from Piura and Lima on the Pacific. The Piura locality (Huanabamba), however, is in the Amazonian drainage. De la Puente (1951) mentioned Libertad (Machi at 3000 m.) on the Pacific side. The American Museum also has specimens from Huánuco (Cerros del Sira, AMNH 233342-46, 233352, 236032) and Ayacucho, whereas the Field Museum has specimens from Apurímac. The presence of this species on both sides of the Andes is hardly surprising in view of the elevational range of ca. 300 to 2750 m. that Tuttle indicated. The Terborgh and Weske collections carry this species to 3370 m. in Ayacucho (Puncu, AMNH 233347) and 3540 m. in Cuzco (Cordillera Vilcabamba summit, AMNH 233302-03). The Louisiana State University even has specimens from 3600 m. in Ayacucho (Cusimachi). These are the very highest altitudes from which bats were obtained by their expeditions and considerably higher than the minimum needed to get through the Andean passes.

[*Choeroniscus inca* (Thomas)]—Tuttle recorded this bat in Peru only from Puno (ca. 400 m.). The systematics of small South American *Choeroniscus*, however, is very confused. Goodwin and Greenhall (1961, p. 249) said, "The exact status of *Choeroniscus minor* (Peters) from Surinam cannot be determined, as the type was destroyed during the second World War. The sex of the type is not known and cranial measurements have not been published. If the type of *C. minor* was a female, then it could be closely allied to *C. intermedia*, but if a male, it could be close to or the same as the specimens we now know as *Choerniscus inca* (Thomas), because males of that species are considerably smaller than females. The forearm length in male specimens of *C. inca* is about the same as in females of *intermedia*." However, Husson (1962, pp. 133-135) examined the type which was still in the Stuttgart Museum. It is an adult male and according to Goodwin and Greenhall's reasoning should be of the same species as *inca*. Husson also gave external and skull measurements, correcting some errors in Peters' original description. The forearm length of the male type of *minor* (34.8) compares with Goodwin and Greenhall's meas-

urement of a male *intermedius* (33.5). The corresponding measurements for greatest length of skull are 21.9 and 21.4. Thomas (1912) gave a forearm length of 33 for the type (male) of *inca*, but gave no skull length measurement, probably because the skull was broken. The forearm length given is surprisingly short considering that the maxillary tooth row length is given as 7.8 as opposed to 7.7 for the type of *minor* and 7.5 for Goodwin and Greenhall's male *intermedius*. I am therefore inclined to think that Thomas measured the forearm in a different way than did Goodwin and Husson. Study of a number of skulls of *Choeroniscus* from Trinidad, British Guiana, Brazil, Peru, and Ecuador have convinced me that two species can be distinguished. These specimens include all that were available to Goodwin and Greenhall, among them the type of *intermedia*. Since females are larger than males, the sexes must be compared separately. That plus the extreme fragility of the skulls and the greatly reduced and probably nearly functionless dentition is presumably responsible for the present confusion. Nevertheless, the two species can be distinguished by rostral length, which is reflected by maxillary tooth row length. Thomas (1912) distinguished *inca* from *minor* solely by the relative sizes of the premolars and molars. On the basis of these skulls, I can see considerable variation in this character, but no clear-cut distinction between two forms. The species with the longer rostrum would then be called *C. minor* (*inca* a synonym) and the species with the shorter rostrum would stand as *C. intermedia*. I will therefore treat the Peruvian records of *Choeroniscus* under these two names. The formal synonymy of *Choeroniscus minor* would therefore stand:

Choeronycteris minor (Peters), 1869, p. 366. Type locality, Surinam.

Choeronycteris inca (Thomas), 1912, p. 403. Type locality, Rio Yahuarmayo, Puno, Peru.

Choeroniscus intermedius (J. A. Allen and Chapman)—Tuttle recorded this species only from Pasco. The American Museum has no other Peruvian specimens. The species is apparently confined to the Amazonian lowlands.

Choeroniscus minor (Peters)—Tuttle recorded

this Amazonian lowland species only from Loreto and Pasco. However, if *inca* is considered a synonym as is here recommended, the species is also known from Puno. The American Museum has no other Peruvian material.

Lichonycteris obscura Thomas—Tuttle recorded this species only from the Amazonian lowlands of Pasco, Gardner (1976) from Loreto. The American Museum has no Peruvian specimens.

Carollia castanea H. Allen—Unlike the other two South American species of the genus, *C. castanea* presents no identification problems once the characters used by Pine (1972) are understood. Almost confined to the Amazonian lowlands, *C. castanea* was recorded from Loreto, Pasco, and Junín by Tuttle (1970) and from Huánuco by Pine (1972). The American Museum has specimens from Ayacucho (Santa Rosa, AMNH 233353-57) and Cuzco (Rio Apurimac, AMNH 233374, and Rio Mapitunari, AMNH 233386, 233388, 233390-94, 233397-403). A Field Museum record from Chanchamayo (1100 m.) appears to be the highest record for Peru.

Carollia perspicillata (Linnaeus)—Until recently, only two species of *Carollia* were recognized from South America. Pine (1972), however, recognized three and as a result, a check of all specimens of *Carollia* in the American Museum has been undertaken, particularly those from Peru (none of which were examined by Pine). I have had no difficulty, separating out *castanea* (as mentioned above) but separating the other two has proved to be much more difficult. All of Pine's skull characters are of some value, but none are completely diagnostic, and some are rather subtle. Therefore, while I am reasonably confident about most of my identifications, it is possible that I have misidentified some. With this note of caution, the distributional patterns of the two species in Peru may be compared. Tuttle recorded *C. perspicillata* from Loreto, Pasco, Junín, and Puno. The localities referred to by Tuttle are all on the eastern slope. Pine (1972), however, referred to specimens from Madre de Dios, San Martín, Huánuco, and Cuzco on the Amazonian side and Tumbes on the Pacific side. Additional records from the literature are suspect,

as Tuttle mentioned, since they may actually pertain to *C. brevicauda*. The American Museum, however, also has specimens from Amazonas (mouth of the Cenipa River, AMNH 98745, 98749, 98752, 98755), Ayacucho (Santa Rosa, 800 m., AMNH 233446-55), and Cajamarca (Perico, AMNH 67091-93). The altitude of Perico is not given but is probably at ca. 500 m. While clearly not restricted to the lowlands, the upper altitudinal limit of *C. perspicillata* is uncertain due to confusion with *C. brevicauda*. The highest that Pine gave for specimens he listed is ca. 750 m. (Yurac Yacu in San Martín), but the American Museum has a specimen collected by Schunke at 1200 m. (Chanchamayo in Junín). The Weske and Terborgh expeditions obtained it as high as 1270-1550 m. (Cordillera Vilcabamba, west side) in Cuzco and 1285-1330 m. (Cerros del Sira) in Huánuco. Thomas (1927b) and Sanborn (1951) recorded it from ca. 1500 m. (Chihuangala in Huánuco; Hacienda Cadena in Cuzco), but the specimens could be referable to *C. brevicauda*.

Carollia brevicauda (Schinz)—This is the species that Tuttle called *Carollia subrufa*. He recorded it only from Cuzco, but Pine (1972) recorded it also from Loreto, Madre de Dios, Huánuco, Junín, and Puno. In addition, the American Museum has specimens from Pasco (Loma Linda, AMNH 213309; Nevati, AMNH 239901; San Juan, AMNH 230384, 230388, 230392-93) and Ayacucho (Estera Rohuana, AMNH 233371-73; Huanhuachayo, AMNH 233358-70, 233435-45), some of those from Pasco having been listed as *perspicillata* by Tuttle (based on earlier museum identifications). All known Peruvian localities for *C. brevicauda* are on the Amazonian side of the Andes and some are definitely in the lowlands, though here *perspicillata* is usually far more common. *Carollia brevicauda* is known, however, from altitudes considerably higher than the highest known for *C. perspicillata*. Tuttle (1970) and Pine (1972) both give Idma (ca. 1850 m.) in Cuzco as the highest Peruvian locality. Weske and Terborgh, however, obtained *C. brevicauda* from several higher altitudes, the highest being 2065-2260 m. on the Cordillera Vilcabamba (in Cuzco). The Field

Museum has a specimen from Limapuncu (2400 m.) in Cuzco. Clearly, therefore, *brevicauda* extends well above 2000 m., almost high enough to be able to transverse the lowest passes of the Andes in northern Peru, though it is not known to have done so.

Rhinophylla pumilio Peters—Tuttle recorded this Amazonian lowland species from Loreto, San Martín, and Pasco. The American Museum has specimens from Huánuco (Rio Llullapichis, AMNH 233520-25, 236054-58; 15 km. NNE Tingo Maria, AMNH 216110). The highest altitude for Peru is ca. 750 m. (Yurac Yacu in San Martín).

Rhinophylla fischeri Carter—Tuttle recorded this rather rare Amazonian lowland species from Loreto and Pasco. The American Museum has specimens from Huánuco (Cerros del Sira at 690 m., AMNH 236049; Rio Llullapichis, AMNH 233519, 233863-64, 236050-53).

Sturnira bidens (E. Geoffroy)—This species is known only from the highlands of the eastern slope of the Andes in Ecuador and Peru. Tuttle recorded this species only from Huánuco, but the American Museum has specimens from Ayacucho and Cuzco which were reported by Gardner and O'Neil (1971). All known localities lie between 1990 m. (Estero Rohuana in Ayacucho) and 2825-2845 m. (Cordillera Vilcabamba, west side, in Cuzco).

Sturnira nana Gardner and O'Neil—This species was described, since Tuttle's work (Gardner and O'Neil, 1971), from Huanhuachayo (1660 m.) in Ayacucho. The American Museum has four specimens from the only known locality, which is on the Amazonian slope considerably below the lowest known altitude for *S. bidens*.

Sturnira erythromos (Tschudi)—Tuttle recorded this species from Huánuco and Cuzco. The American Museum has specimens from Ayacucho (Huanhuachayo, AMNH 233529, 233594-95, 233597) and the Field Museum from Junín (Huancipistana, Tarma). While there are no altitudinal data for some of the Cuzco specimens, all known Peruvian material appears to come from the highlands of the Amazonian slope. Altitudes for American Museum specimens (mostly from Weske and Terborgh) run from a low of 1285-1330 m. (Cerros del

Sira in Huánuco, AMNH 233540) to a high of 3540 m. (Cordillera Vilcabamba summit in Cuzco, AMNH 233530-31, 233600-01, 233604). The latter is the highest altitude from which Weske and Terborgh obtained bats. The Louisiana State University Museum of Zoology has a specimen from 3600 m. in Ayacucho (Cusimachi).

Sturnira lilium (E. Geoffroy)—Tuttle recorded this common Amazonian species from Madre de Dios, Pasco, Junín, and Cuzco. The American Museum has specimens from Loreto (Boca Rio Curaray, AMNH 71691-95) and Huánuco (Cerros del Sira, AMNH 233586). The Louisiana State University Museum of Zoology has a specimen from Ayacucho (Huanhuachayo) at 1660 m., which, if correctly identified, may be the highest for Peru. The Texas Cooperative Wildlife Collection also has a specimen from Piura on the Pacific side.

Sturnira ludovici Anthony—Tuttle recorded this species from Pasco, Junín, and Cuzco. The American Museum has specimens from Huánuco (Cerros del Sira, AMNH 233579-85) and Ayacucho (Estero Rohuana, AMNH 233550, Huanhuachayo, AMNH 233551-61, 233592-93, 233596). Tuttle gave an altitudinal range in Peru (based on his own collections) of from lower than 300 m. to ca. 2200 m. and this agrees very well with the range of altitudes from which Weske and Terborgh obtained *S. ludovici*. The Amacho (Cuzco) locality mentioned by Tuttle, however, is at ca. 2750 m. However, despite its altitudinal range, in Peru the species is known only from the Amazonian slope.

Sturnira magna de la Torre—This is another species with a limited known range on the Amazonian slope from Colombia to Peru. Tuttle recorded it from Loreto and Pasco, all localities being in the lowlands. The American Museum has specimens from Huánuco (Cerros del Sira, AMNH 236059-60, 233588-90) and Cuzco (Cordillera Vilcabamba, west side, AMNH 233587, 214347), however, and these range from the lowlands up to 2065-2260 m. Gardner (1976) also recorded this species from a relatively high altitude (ca. 1660 m.) in Ayacucho. It seems odd that a species should have so narrow a geographical and so wide an altitudinal range.

Sturnira tildae de la Torre—This rather rare Amazonian lowland species was recorded by Tuttle (1970) from Loreto and Pasco. The American Museum has a specimen from Huánuco (Rio Lullapichis, AMNH 233591).

Uroderma bilobatum Peters—Tuttle recorded this species from Loreto, Pasco, and Cuzco on the eastern side of the Andes and from Tumbes on the western side. The American Museum also has specimens from Amazonas (Pomara, AMNH 69230-31, see Vaurie, 1972, p. 27), San Martín (Santa Rosa de Huayabamba, ca. 1850 m., AMNH 11837-40, 118442, erroneously allocated to *Vampyrops lineatus* by Allen (1897a) and reported by Tuttle), Huánuco (Cerros del Sira at 860 m., AMNH 233609-10 and at 1535-1570 m., AMNH 233608), and Junín (Rio Ene, AMNH 233611-12). The Field Museum also has specimens from Ayacucho (Sivia). The altitudinal distribution is therefore from the lowlands to over 1800 m., almost high enough to get over the lowest passes in the Andes, and its presence on the Pacific side is therefore not unexpected. Davis (1968) put both Amazonian and Pacific populations into the same subspecies (*U. b. thomasi*).

Uroderma magnirostrum Davis—This Amazonian lowland species was recorded by Tuttle only from Loreto. The American Museum has no other Peruvian specimens.

Vampyrops dorsalis Thomas—Tuttle (1970) recorded this species only from Cuzco, but Gardner and Carter (1972b) recorded it also from Huánuco and Ayacucho. All American Museum Peruvian material comes from these three Departments, all localities being on the Amazonian slope. In Peru, the species certainly has a very extensive ecological range from the upper part of the lowlands at 860 m. (Cerros del Sira, AMNH 233640, in Huánuco) to the highest elevation from which Weske and Terborgh obtained bats at 3540 m. (summit of Cordillera Vilcabamba, AMNH 233615, in Cuzco).

Vampyrops lineatus (E. Geoffroy)—Tuttle's record of this species in Peru is erroneous (see *Uroderma bilobatum* account above). However, I believe that the form described by Gardner and Carter (1972a) as *nigellus* is actually a subspecies of the allopatric *V. lineatus*, based on similarity in skull characters. Except for

darker color, which I consider a poor taxonomic character in bats, the characters of *nigellus* which Gardner and Carter (1972b) listed (shorter forearm, broader rostrum, longer maxillary toothrow) are all measurements which overlap with those of *V. l. lineatus* from Mato Grosso (Brazil) and Bolivia. The formal synonymy of *Vampyrops lineatus* would therefore stand:

Phyllostoma lineatum E. Geoffroy, 1810, p. 180.

Type locality, Asunción, Paraguay.

Vampyrops lineatus sacrillus Thomas, 1924a, p. 236. Type locality, Rio Doce, Espirito Santo, Brazil.

Vampyrops nigellus Gardner and Carter, 1972a, p. 1.

Type locality, Huanhuachayo, Ayacucho, Peru.

Vampyrops lineatus nigellus was recorded by Gardner and Carter in Peru only from Huánuco and Ayacucho at elevations of from 850 to 2400 m. The American Museum also has specimens from Cuzco. All of our specimens were collected by Weske and Terborgh and range from a low of 600 m. (Hacienda Luisiana, AMNH 233865, in Ayacucho) to a high of 2640 m. (Cordillera Vilcabamba, west side, AMNH 233685, in Cuzco). Its lower limit may be similar to that of *V. dorsalis* but it does not seem to get nearly as high.

Vampyrops infuscus Peters—Tuttle included this species in *V. vittatus* but I agree with Gardner and Carter (1972b) that they should be separated. I have not seen the specimens from San Juan (Pasco) which Tuttle referred to *vittatus*, but the American Museum now has the San Ramón (Junín) specimens and they are clearly *infuscus*. Since San Juan (ca. 300 m.) would be a considerable downward extension of altitudinal range for *vittatus*, but is well within the altitudinal range of *infuscus*, I think it far more likely that the San Juan specimens are *infuscus* rather than *vittatus*. Another consideration is that there is a considerable difference between the two species, which I would certainly expect Tuttle to recognize if he had both in hand. Therefore Pasco and Junín are considered to be within the range of *V. infuscus*, both localities being on the Amazonian slope. The original type locality is in Cajamarca (Hacienda Ninabamba) and is stated by Tuttle to be "west of the Andes." Since the

holotype was destroyed, Gardner and Carter have designated a neotype, although this would appear to be quite unnecessary. A complication is that the neotype is from near Tingo Maria (Huánuco) on the Amazonian slope and therefore some distance from and (if Tuttle is correct) on the opposite slope from the original type locality, a most unsettling state of affairs. Besides Huánuco, Gardner and Carter recorded this species also from Loreto and Ayacucho. The American Museum has a specimen from Cuzco (Cordillera Vilcabamba, west side, AMNH 233717); specimens from this Department also were recorded by Sanborn (1951) under the name of a junior synonym (*fumosus*). The Field Museum has a specimen from Madre de Dios. The localities for which altitudinal data are available range from less than 200 m. (Curaray River mouth in Loreto, AMNH 71696-701, 71708) to 1285-1330 m. (Cerros del Sira in Huánuco, AMNH 233726-27, 233729). Sanborn's Cuzco record (Hacienda Cadena) if actually collected at this place would carry the altitudinal distribution to ca. 1500 m. Unfortunately there seem to be no altitudinal data for Sanborn's (1941) record (also under the name *fumosus*) from Vitoc Valley, Tarma province, Junín. If the species does indeed reach the Pacific slope (at the type locality), however, one would expect *V. infuscus* to go considerably higher than existing records indicate.

Vampyrops vittatus (Peters)—It appears that all Peruvian records of this species prior to Gardner and Carter (1972b) actually pertain to *V. infuscus*. True *vittatus* was recorded by Gardner and Carter from several localities in the highlands of the Amazonian slope in Huánuco and Ayacucho. The American Museum has a specimen from Cuzco (Cordillera Vilcabamba, west side, AMNH 214360). The altitudinal range in Peru given by Gardner and Carter is 1000-2600 m. All 10 Huánuco specimens in the American Museum (Cerros del Sira) fall within this range, but the Cuzco specimen is from 3170-3320 m. In spite of this, *V. vittatus* is not known to reach the Pacific slope.

Vampyrops helleri Peters—The bats referred to by Tuttle (1970) actually belong to two species, true *helleri* and *brachycephalus*. Both are lowland species and were distinguished by Rouk and Carter (1972) and by Handley and

Ferris (1972). Gardner and Carter (1972b) listed *V. helleri* from Loreto and Huánuco. Tuttle's Junín (Rio Seco) specimen (now in the American Museum, which has other Junín specimens) is *helleri* but not his Pasco specimens. The American Museum also has specimens of *helleri* from Cuzco (Luisiana, AMNH 208071, and Apurímac, AMNH 233641). I have studied the three specimens from Tumbes (on loan from the Field Museum) mentioned by Tuttle (1970) and identify them as *helleri*. However, when compared with American Museum specimens from Junín and Cuzco, they are larger (condylobasal 9.7-10.5 vs. 8.1-9.2) and lack any trace of an accessory cusp on the anterior margin of the posterior lower premolar which all four of the Peruvian Amazonian skulls have to a greater or lesser degree. If subspecies can be recognized in *V. helleri*, the Tumbes specimens should be referable to *V. h. helleri* of Middle America and the Amazonian to *V. h. incarum*. Gardner and Carter gave the altitudinal limits of *V. helleri* as 150 to 860 m. All Peruvian specimens of *helleri* in the American Museum fall within these limits.

Vampyrops brachycephalus Rouk and Carter—This species was described almost simultaneously by Rouk and Carter (1972—*brachycephalus*) and by Handley and Ferris (1972—*latus*). As Carter and Rouk (1973) pointed out, these two names are synonyms, *brachycephalus* having 18 days' priority. Between them, the two papers recorded this Amazonian lowland species from Loreto, Huánuco, and Pasco. All the American Museum specimens are from Loreto and Pasco, but the Field Museum has specimens from Cuzco. Gardner and Carter (1972b) gave the altitudinal range in Peru as 150 to 740 m. The American Museum specimens from Loreto (Orosa, AMNH 73990-93, 74013; Mazan River, AMNH 98770, 98782) are only slightly lower.

Vampyrodes caraccioli Thomas—This Amazonian lowland species was recorded by Tuttle from Loreto, Pasco, and Junín. The San Ramón (Junín) record at ca. 900 m. appears to be the highest for Peru. The American Museum has no Peruvian specimens other than Tuttle's, but the Field Museum has specimens from Cuzco.

Vampyressa bidens (Dobson)—The only definite localities from which Tuttle (1970) recorded this species are in Loreto. The American Museum has specimens from Huánuco (Cerros del Sira, AMNH 233736-37, 233785) and Cuzco (Cordillera Vilcabamba, AMNH 214351, 233734-35, and Luisiana, AMNH 208072). One of the Cordillera Vilcabamba specimens, collected at 890 m. appears to be the highest record for Peru.

Vampyressa melissa Thomas—Tuttle recorded this species only from the type locality at ca. 2200 m. in Amazonas. The American Museum, however, has two specimens from somewhat lower (1535-1570 m.) in Huánuco (Cerros del Sira, AMNH 233761, 233769) and Gardner (1976) recorded it from still lower (ca. 1000 m.) in Ayacucho. Aside from the inference that it is probably confined to the highlands of the Amazonian slope of Peru, little can be said about the geographical or altitudinal range of this species.

Vampyressa pusilla (Wagner)—This Amazonian species was recorded by Tuttle only from Loreto and Cuzco. The only Peruvian specimens in the American Museum are from Loreto. The Cuzco record (Hacienda Cadena) is at 1500 m., indicating that the species occurs in the highlands as well as the lowlands.

Chiroderma trinitatum Goodwin—Tuttle recorded this Amazonian lowland species from Loreto and Pasco, Gardner (1976) also from Ayacucho. The Texas Cooperative Wildlife Collection has a specimen from Huánuco and the Field Museum has specimens from Cuzco. The altitude of one of the two localities in Ayacucho (1000 m.) is the highest Peruvian record. The American Museum has no Peruvian material other than Tuttle's Pasco specimen.

Chiroderma villosum Peters—Tuttle recorded this Amazonian lowland species only from Loreto and Pasco. Thomas (1927a) recorded it from San Martín (Yurac Yacu at 800 m.). The American Museum has single specimens from Junín (Rio Ene, AMNH 233739) and Cuzco (Rio Mapitunari, AMNH 233738).

Ectophylla macconnelli (Thomas)—Tuttle's records of this species are all from the Amazonian lowlands of Loreto, Pasco, and Cuzco. The American Museum also has lowland mate-

rial from Loreto and Cuzco, which is referable to the Amazonian subspecies (*E. m. macconnelli*). In addition, the American Museum has highland specimens from Cuzco (Cordillera Vilcabamba, west side, at 1270-1550 m., AMNH 214368) and Huánuco (Cerros del Sira at 1535-1570 m., AMNH 233745-49) which are referable to the Trinidadian subspecies (*E. m. flavescens*). (See Goodwin and Greenhall, 1962, for the characters which distinguish these subspecies.) What, if any, geographical connection exists between the Trinidadian and Peruvian populations is unknown. Obviously any populations in the mountains of Venezuela, Colombia, or Ecuador should be carefully scrutinized.

Artibeus (Enchisthenes) harti Thomas-Tuttle (1970) did not record this species, but the American Museum has a number of specimens collected by Weske and Terborgh from Cuzco (Cordillera Vilcabamba, AMNH 214367, 233602-03, 233753, 233795-99) and Ayacucho (Huanhuachayo, AMNH 233791-92). All are in the highlands of the Amazonian slope from a low of 1660 m. (Huanhuachayo) to a high of 3540 m. (Cordillera Vilcabamba summit). At the latter locality (the highest from which Weske and Terborgh obtained bats), it was one of four species of bats collected and was fairly common (seven specimens out of 15 for all four species obtained at that locality). However, Gardner (1976) recorded the species from a relatively low altitude (ca. 850 m.) in Junín.

Artibeus cinereus (Gervais)—The problem of species among the small *Artibeus* of South America has been a knotty one as a comparison with Andersen (1908), Osgood (1916), Thomas (1924b, 1928), Hershkovitz (1949), and Davis (1969, 1970a) made clear. However, except for *anderseni* (see below) and the very different *A. hartii*, I am inclined to agree with Hershkovitz (1949) in referring all small South American *Artibeus* to *A. cinereus*. Certainly, I believe that the two forms described from Peru (*glaucus* and *pumilio*) should be so allocated. Dr. Charles Handley is currently revising the small South American *Artibeus* and I have discussed with him some of the problems involved. However, it should be emphasized that my conclusions are *not* necessarily his. The two characters on which Andersen (1908, p.

315) and Davis (1969) relied most heavily are the size of the postero-internal cusp of M^1 (probably the hypocone) and the presence or absence of the small m_3 . Hershkovitz (1949) has criticized the value of both these characters in Ecuador, Colombia, and Venezuela. The picture in the Amazon basin (as shown by the American Museum specimens) is basically similar. The size of the hypocone, whether based on the size of the cusp (Andersen) or on the extent of the hypocone area (Davis) shows a great deal of erratic variation not correlated with other characters, and in my opinion it has no taxonomic value, at least in Peru and other parts of western Amazonia (specimens examined from Ecuador, Venezuela, Bolivia, and Brazil). The presence or absence of m_3 shows less intrapopulational variation (and in my material is always either present or absent on both sides). Specimens from Brazil near the boundary of the states of Pará and Amazonas (Faro; Villa Bella Imperatriz) resemble *A. cinereus* from farther east in lacking the third lower molar, but are smaller (condylobasal length 16.8-17.0 vs. 17.3-18.0). Single specimens from northeastern Bolivia (4 km. above Costa Marques; Versalles) and Amazonian Ecuador (Canelos) and series from Amazonian Venezuela (Esmeralda; Caño Leon) and from a lowland locality in the Peruvian Department of Junín (Santa Rosa, AMNH 76089, 76098) are likewise small (condylobasal length 16.4-17.0) but apparently always have the third lower molar. To me they seem best referred to *A. c. pumilio*, whose type locality is in Loreto, but Handley (1976, p. 33) called this "*Artibeus* sp. A." Specimens from localities above 650 m. in Huánuco (Cerros del Sira, 36 specimens), Ayacucho (Estera Rohuana, AMNH 233750, Huanhuachayo, AMNH 233751), Cuzco (Cordillera Vilcabamba, 12 specimens), and Puno (Inambari River, AMNH 37197, 37199, Santo Domingo, AMNH 42401), likewise almost always possess the third lower molars but are usually larger (condylobasal length 16.6-18.3) and are here referred to *A. c. glaucus*, whose type locality is at ca. 900 m. in Junín. The formal synonymy of *Artibeus cinereus* would therefore stand (including only named forms of whose placement I am reasonably confident):

- Dermanura cinerea* Gervais, 1856, p. 36. Type locality, Para, Brazil.
Artibeus glaucus Thomas, 1893, p. 336. Type locality, Chanchamayo, Junín, Peru.
Artibeus Watsoni Thomas, 1901b, p. 542. Type locality, Bugaba, Chiriqui, Panama.
Artibeus pumilio Thomas, 1924b, p. 531. Tushemo, near Masisea, Loreto, Peru.

Of the records Tuttle (1970) cited, the Junín record is of *A. c. glaucus*, the Thomas (1924b, 1928) Loreto records are presumably both *A. c. pumilio*, but in my opinion Tuttle's Pasco record and probably Pirlot's (1968) Loreto record are *A. anderseni*. As indicated above, the American Museum has specimens from Huánuco, Junín, Ayacucho, Cuzco, and Puno. Weske and Terborgh obtained this species from a number of localities ranging in altitude from the lowlands to ca. 2640 m. (Cordillera Vilcabamba, west side).

Artibeus anderseni Osgood—In my opinion Tuttle confused this species with *A. cinereus*, but after study of many Amazonian specimens from Brazil, Venezuela, Bolivia, Ecuador, and Peru, I am convinced that two species are involved. Besides its shorter face and more abrupt forehead, *A. anderseni* apparently always lacks the last lower molars, which *A. cinereus* in western Amazonia almost always has.

Artibeus anderseni was first described by Osgood (1916); the American Museum has two paratypes from Porto Velho, Brazil: comparison of these specimens with others shows that *anderseni* occupies an extensive range in western Amazonia. I therefore refer Peruvian specimens to *A. anderseni*. The name *nanus*, used by Pirlot (1968) for his Loreto specimens, is currently considered (Davis 1970a) to be the name for a Mexican subspecies of *A. phaeotis*, which is strikingly similar to *A. anderseni*. Much of the special resemblance disappears, however, when specimens of *A. phaeotis* from Panama and northwestern South America are compared with *A. anderseni*. All Peruvian specimens of *A. anderseni*, as far as is known, are from the lowlands of Loreto (six AMNH specimens from Boca Rio Curaray, Lagarto, Mazan River, Puerto Indiana, and Sarayacu), Huánuco (four AMNH specimens from Rio Llullapichis, Mon-

tealegre, and 15 km. NNE of Tingo Maria), Pasco (five AMNH specimens from Nevati, San Juan, and San Pablo), and Cuzco (Rio Mapitunari, AMNH 233759-60), ca. 700 m. (15 km. NNE Tingo Maria, AMNH 216115) in Huánuco being the highest known. The Pasco specimens are in part from Tuttle, who identified them as *cinereus*.

Artibeus concolor Peters—Tuttle made no mention of this rare Amazonian lowland species, but Gardner (1976) recorded it from Loreto. The American Museum has no Peruvian specimens.

Artibeus fraterculus Anthony—Tuttle did not distinguish this species from *A. jamaicensis*, but study of specimens of the *jamaicensis-lituratus* group from western Ecuador and western Colombia reveals that north of about 2 degrees South, there are only typical *lituratus* (related to *l. intermedius* and *l. palmarum*) and a large *jamaicensis* (related to *j. richardsoni* to which the name *aequatorialis* applies). Farther south, however, there is a third species, similar to *A. jamaicensis* (as it exists in western Ecuador) in the absence of postorbital processes in the frontal region, in its relatively narrow zygomatic breadth, and in the absence of third upper molars, but much smaller in overall size. This is the species that Anthony (1924) named *A. fraterculus*. It is this third species that appears to be the only *Artibeus* with an extensive distribution on the Pacific side of Peru. Tuttle recorded it from Tumbes, Piura, and Lambayeque, all on the western side of the Andes. De la Puente (1951), however, recorded it (as a subspecies of *A. jamaicensis*) both from Lima on the Pacific side and Cajamarca on the Amazonian side. The elevation of this last locality ("Prov. Hualgayok: grutas de Ninabamba") is not given, but is presumably in an isolated arid portion of the Amazon basin. Finally Patten (1971) recorded the species from a similar area in Amazonas. The American Museum has no Peruvian specimens.

Artibeus fuliginosus Gray—The present taxonomic situation regarding the large *Artibeus* (*jamaicensis-lituratus* group) in South America east of the Andes is a very confused one. In southern Central America, there are two species differing both in size and in degree of develop-

ment of postorbital processes and associated flattening of the rostrum. I agree with Davis (1970b) that the large species with well-developed post-orbital processes should be called *A. lituratus* while the other species is *A. jamaicensis*. Both species occur essentially unchanged in western Colombia where they agree in normally lacking the last upper molar. East of the Andes, the picture is more complex. Besides *lituratus*, which remains essentially the same, there are two species, both of which agree with *jamaicensis* in having poorly developed postorbital processes and rostra which are rounded on top. They agree with each other but differ from *jamaicensis* of Central America and western Colombia in normally possessing the last upper molars. These two eastern species differ markedly in size, the larger agreeing with *lituratus*, at least in skull length, whereas the other is smaller than western Colombian *jamaicensis*. The names *fallax* and *hercules* appear to be applicable to the large form, whereas *fuliginosus* and *trinitatis* apply to the small one. These three eastern species have been combined by some in various ways. Hershkovitz (1949) combined *fallax* with *A. lituratus*, but included *trinitatis* in *A. jamaicensis*. Tuttle (1970), on the other hand, judged by the specimens he refers to, evidently included *fallax* in *jamaicensis*, but explained that he believed that two species are involved. If this is true (and I agree), the question arises as to which of these two eastern species (besides *A. lituratus*) represents the western *jamaicensis*. I believe that it is the smaller (*trinitatis*, *fuliginosus*), which represents the western *A. jamaicensis*, for two reasons. First, the size difference is less between the small form and western *A. jamaicensis* than between the large form and western *jamaicensis*. Second, there appears to be a wide hiatus between the ranges of the large form (no specimens in the American Museum closer than northwestern Venezuela) and western *A. jamaicensis*, whereas the smaller form (represented by *trinitatis*) occurs in the Departments of Magdalena, Cundinamarca, and Tolima. Provisionally, I would be inclined to allocate specimens from central and north-eastern Colombia, northern Venezuela, Trinidad, Tobago, and Grenada to *A. j. trinitatis*

and specimens from the Amazon-Orinoco basins and the Guianas to *A. j. fuliginosus*. Patten (1971), however, treated *fuliginosus*, which he redescribed, as a new species, and considered that the larger, rather than the smaller, of the two Amazonian forms represents *jamaicensis* (though he considered them separate species). However, in view of the uncertainty and the fact that Handley (1976, p. 31) also recognized *fuliginosus* as a separate species, I reluctantly keep *fuliginosus* separate, especially since Davis and Dixon (1976) used this name for Peruvian specimens. Because of the composite nature of Tuttle's *jamaicensis*, it is difficult to allocate his references. He indicated, however, that the smaller of the two Amazonian species included under *jamaicensis* (therefore presumably *fuliginosus*) was represented in his material only by specimens from Pasco (San Juan). The American Museum specimens that I would allocate to *A. fuliginosus* came from Loreto (Boca Rio Curaray, AMNH 71441, 71473-74, 71702, 71711), Amazonas (Cenipa River mouth, AMNH 98751, 98753), Huánuco (Cerro del Sira and vicinity, 27 AMNH specimens), Pasco, Junín (Rio Ene, AMNH 233823-30, Santa Rosa, AMNH 76083), and Cuzco (Mapitunari, AMNH 233803-11). The Field Museum has a specimen from Piura, but the locality (Huancabamba) is still on the Amazonian slope. The species is known to range from the lowlands to 1285-1330 m. (Cerro del Sira, AMNH 233812).

Artibeus planirostris (Spix)—I have explained above what my concept of this species is (the large form with poorly developed postorbital processes). Following Patten (1971) this species is called *A. planirostris*. Specimens from Amazonian Ecuador and Peru tend to be larger than those of the Guianas (*p. fallax*) and of Amazonian Brazil and Bolivia and the name *hercules* is available for the larger western populations. Tamsitt and Valdivieso (1966) discussed the characters of *hercules* and while I do not agree with their interpretation (probable synonymy with *A. l. lituratus*), they have made clear that *hercules* does possess the last upper molar. Surprising as it may seem, this character separates *fallax* from *lituratus* quite effectively in Peru and I therefore agree with Patten (1971) in

associating *hercules* with *fallax* rather than with *lituratus*. The formal synonymy would therefore stand (including only named forms of whose placement I am reasonably confident):

Phyllostoma planirostre Spix, 1823, p. 66. Type locality, suburbs of Salvador, Bahia, Brazil.

Artibeus fallax Peters, 1866a p. 355. Type locality, Surinam.

Artibeus hercules Rehn, 1902, p. 638. Type locality, "eastern Peru."

Uroderma validum Elliot, 1907, p. 537. Type locality, Cayenne, French Guiana.

Since Tuttle stated that the smaller Amazonian species he included in *jamaicensis* were obtained only at San Juan, it follows that the larger species (here called *planirostris*) was the one collected at the other localities from which he had specimens. These are all in the lowlands of Pasco and Junín. The American Museum has specimens from Loreto (Boca Rio Curaray, AMNH 71703-07), Huánuco (Cerros del Sira and vicinity, 18 AMNH specimens), Ayacucho (Santa Rosa, AMNH 233801-02, 233832-33), and Puno (Inambari River, AMNH 37195). Osgood (1914) recorded "*planirostris fallax*" from San Martín (Moyobamba, 820 m.) and Patten (1971) recorded the species from Cajamarca (Rio Chunchuca). Altitudes range from below 200 m. to 1660 m. (Huahuanchayo in Ayacucho, AMNH 233831).

Artibeus lituratus (Olfers)—As indicated above, I regard *hercules* as a subspecies of *A. planirostris* rather than of *A. lituratus*, which in Peru is represented by *A. l. lituratus*. Tuttle recorded *A. lituratus* from Loreto, San Martín, Huánuco, and Pasco. The American Museum has specimens from Amazonas (Santa Rosa, AMNH 69226-28) and Cajamarca. All these localities are in the Amazonian drainage, but Patten recorded this species not only from Madre de Dios and Cuzco in the Amazonian lowlands, but also from Tumbes on the Pacific coast. While the locality with greatest known recorded altitude (Cerros del Sira at 1120 m., AMNH 236095-96) is in Huánuco, the Cajamarca locality (Jaen, AMNH 69229) is at ca. 2000 m.

Sphaeronycteris toxophyllum Peters—Tuttle recorded this rare Amazonian lowland species only from Loreto. The American Museum also has a specimen from Loreto.

Desmodus rotundus (E. Geoffroy)—This common widespread species was recorded by Tuttle from Pasco and Junín and by de la Puente (1951) from Loreto, San Martín, Huánuco, Ayacucho, Cuzco, Puno, Cajamarca, Piura, La Libertad, and Lima. Thomas and St. Leger (1926) recorded the species from Amazonas, the American Museum has two specimens from Ica (Chincha islands, AMNH 60603, and Vieja island, AMNH 60604), and the Field Museum has specimens from Huancavelica, Apurimac, and Ancash. As Tuttle indicated, the known altitudinal range is from sea level (on both sides of the Andes) to ca. 3500 m. (Lircay in Huancavelica). Probably *Desmodus rotundus* occurs throughout Peru, wherever large wild or domestic mammals or sea birds are found.

Desmodus youngi Jentink—I follow Handley (1976) in merging *Diaemus* with *Desmodus*. Tuttle recorded this rare Amazonian lowland species only from Loreto. The American Museum has no Peruvian specimens.

Diphylla ecaudata Spix—Tuttle recorded this Amazonian slope species from Loreto, Amazonas, San Martín, and Pasco. The American Museum specimens are also from Pasco. The species extends from the lowlands to ca. 2450 m. (Corosha in Amazonas). Although it thus occurs high enough to get across the lower passes in the Andes, it is not known from the Pacific slope.

FAMILY FURIPTERIDAE

Amorphochilus schnablii Peters—Tuttle recorded this species from Tumbes and Arequipa on the Pacific side and from "Amazonas" in an isolated arid portion of the Amazon basin. De la Puente (1951) recorded the species from Piura and Lima, and correctly placed the "Amazonas" locality (Hacienda Limón) in Cajamarca. The American Museum has a specimen from La Libertad (Trujillo, AMNH 165628) and the Field Museum has specimens from Lambayeque. The Pacific coastal populations are currently placed in *A. s. schnablii*, the Cajamarca one in *A. s. osgoodi*.

Furipterus horrens (F. Cuvier)—Tuttle recorded this rather rare Amazonian lowland species only from Loreto. The locality "Rio Disqui" is evidently an error for Rio Pisqui, a

tributary of the Rio Ucayali (see Vaurie, 1972, p. 26). The American Museum has a second specimen from Orosa (AMNH 74108), also in Loreto.

FAMILY THYROPTERIDAE

Thyroptera discifera Lichtenstein and Peters-Tuttle recorded this rare Amazonian lowland species only from Loreto. The American Museum has no Peruvian specimens.

Thyroptera tricolor Spix-Tuttle recorded this common Amazonian species from Pasco and Cuzco; Gardner (1976) from Loreto. The American Museum has specimens from Huánuco (Puerto Marquez, AMNH 67236-37, 67239; Rio Lullapichis, 250 m., AMNH 233849). One of Sanborn's (1951) Cuzco records (Hacienda Cadena at 1500 m.) is apparently the highest record for Peru.

FAMILY VESPERTILIONIDAE

Myotis nigricans (Schinz)—Since Tuttle's 1970 paper, the *Myotis* of South America have been revised by LaVal (1973). LaVal's arrangement is quite different from the one Tuttle used, involving the recognition of seven Peruvian species, in place of the four that Tuttle discussed, and with the reidentification of many specimens. *Myotis nigricans* is the species most affected, since its scope has been considerably reduced by LaVal. I will therefore use LaVal's paper as my point of departure. I have tried to identify all the American Museum *Myotis* specimens from Peru according to LaVal's arrangement, using specimens he studied as a check. In general, I have had no difficulty in separating out the species he split off from *M. nigricans*. I have had difficulty with a few specimens from Cuzco, however, as to whether to call them *M. nigricans* or *M. keaysi*. As a result, there is some uncertainty regarding the upper altitudinal limit of *M. nigricans* on the Cordillera Vilcabamba. LaVal recorded *M. nigricans caucensis* from Loreto, San Martín, Huánuco, Pasco, Junín, Cuzco, Puno, and Cajamarca, all in the Amazonian drainage at elevations of from 100-2000 m. He recorded *M. n. punensis* from Piura on the Pacific slope. The American Museum also has specimens of *M. n. caucensis* from Madre de Dios (Puerto Maldonado, AMNH 145505) and Amazonas

(Cenipa River mouth, AMNH 98747-48, 98750, 98756, 99316), and the Field Museum has specimens of *M. n. punensis* from Lambayeque (Olmos).

All the American Museum specimens are from below 2000 m. except for three from Cuzco (Cordillera Vilcabamba, AMNH 233852, 233855-56), which if correctly identified by me would carry *M. nigricans* to at least 3170 m. Louisiana State University has a specimen identified as *nigricans* from 3370 m. in Ayacucho (Puncu). As indicated above, there is some doubt about these identifications due to possible confusion with *M. keaysi*. Even if these Cuzco and Ayacucho records are ignored, however, the species almost ranges high enough to get over the lowest Andean passes. The subspecies on the two sides are distinct, however.

Myotis atacamensis (Lataste)—LaVal (1973) recorded this species only from Lima and Arequipa on the Pacific slope. The American Museum of Natural History has no other specimens. This species (in Peru) was formerly known as *M. nigricans nicholsoni*. LaVal discussed (but rejected) the possibility that *atacamensis* is indeed only a very small subspecies of *M. nigricans*. Although the size difference between *atacamensis* and *n. punensis* is indeed considerable, it would certainly be very interesting to have specimens from the Pacific slope between northern Piura (Talara and Suyo) and northern Lambayeque.

Myotis keaysi J. A. Allen—This highland species was recorded by LaVal (1973) from Huánuco, Junín, and Puno on the Amazonian side and from Lambayeque (at 1290 m.) on the Pacific slope. The altitudinal range of LaVal's specimens runs from 1100 to 2400 m. The American Museum has specimens from Cuzco (Cordillera Vilcabamba, AMNH 214371, 233850-51, 233853-54, 233857, 236134) and these run from 2640 to 3540 m. The latter is the highest from which Weske and Terborgh obtained bats. It is therefore hardly surprising that the species occurs undifferentiated on the two sides of the Andes.

Myotis albescens (E. Geoffroy)—LaVal (1973) recorded this species from Loreto, Huánuco, Pasco, and Cuzco on the Amazonian side and from Piura on the Pacific slope. The American Museum has a specimen from Ama-

zonas (Cenipa River mouth, AMNH 98754, on the eastern side of the Andes). LaVal gave elevations of from 90 to 1500 m. and the American Museum has no specimens outside this altitudinal range. Thus the maximum known altitude would not permit this species to cross even the lowest passes of the Andes.

Myotis simus Thomas—Most of the specimens Tuttle identified as *simus* are actually *M. riparius*. LaVal (1973) recorded *M. simus* from Loreto, Huánuco, and Pasco, all in the Amazonian lowlands, 600 m. being the highest elevation. The American Museum specimens are from these three Departments and none from any higher elevation.

Myotis riparius Handley—In the past, this species has been confused with both *nigricans* and *simus*, but it is readily identified using the characters of LaVal (1973). LaVal recorded this species from Loreto, Huánuco, and Pasco, all in the Amazonian lowlands, the highest altitude given being only 300 m. The American Museum has specimens from Cuzco (Cordillera Vilcabamba, west side) but from only a little higher (685 m., AMNH 233858-60). The record LaVal gave from extreme southwestern Ecuador suggests that the species may well reach extreme northwestern Peru on the Pacific slope.

Myotis oxyotus (Peters)—LaVal recorded this species from Huánuco, Junín, and Cuzco on the east side of the Andes at elevations of from 1050 to 3120 m. and on the west side in Lima and Ica. The American Museum has specimens from San Martín (Rio Negro at ca. 800 m., AMNH 73215) and Pasco (Rumicruz, ca. 2950 m., AMNH 60597-98), and the Field Museum has the species, which Osgood (1914) called "*Myotis* sp.," from Cajamarca. Thomas (1928) recorded the species from Loreto, but in view of the low elevations (below 200 m.) of the two localities (Cumeria; San Jeronimo), it seems likely that the specimens pertain to one of the four Amazonian lowland species. Clearly the Andes in Peru are not a barrier to this species.

[*Eptesicus andinus* J. A. Allen]—Tuttle recorded this Andean highland species from Huánuco and Junín, since he followed Davis (1966) in regarding it as a species distinct from *E. brasiliensis*. However, after comparing all

American Museum specimens of these two alleged species from Peru and Ecuador, I am inclined to agree with Cabrera (1958) in considering *andinus* as only an Andean highland subspecies of *E. brasiliensis*. Davis (1966) distinguished the two species almost entirely on hair length, the other characters, all external or cranial measurements, showing considerable overlap. Since *andinus* occurs in the cool highlands and *brasiliensis* in the warm lowlands, it would be surprising if *andinus* didn't have longer hair regardless of its taxonomic status. A minor taxonomic problem involves the placement of the name *inca* Thomas (1920). This was described as most closely related to *montosus* but larger. On this basis, Cabrera (1958, p. 107) synonymized *inca* with *montosus*. Tuttle (1970) in the process of clarifying the Department of the type locality (Chanchamayo) accepted Cabrera's synonymy, though Davis (1966) had previously synonymized *inca* with *andinus* (p. 251). Besides the type of *inca* (p. 364), Thomas also recorded *andinus* (which he considered a separate species) from Chanchamayo (p. 361). Davis did not see the type of *inca* but did examine two other specimens in the British Museum [Nat. Hist.] from Chanchamayo (presumably the ones that Thomas had identified as *andinus*); Davis identified them as *montosus chiralensis*. Thus both Thomas and Davis agreed that two species occur at Chanchamayo, but differed in which should be regarded as *andinus* and which should be considered close to *montosus*. This affects the nomenclature of the Peruvian populations of the smaller species since, if Cabrera is right, *inca* (Thomas, 1920) has priority over *chiralensis* (Anthony, 1926). Without a comparison of the three specimens from Chanchamayo with one another and with specimens previously compared with the types of *andinus* and *chiralensis*, it seems impossible to resolve this problem. For the present, however, I follow Davis rather than Cabrera. The formal synonymy of *Eptesicus brasiliensis* (omitting the names listed in synonymy of *E. b. brasiliensis* by Cabrera, 1958, p. 105) would therefore stand:

Vespertilio brasiliensis Demarest, 1819, p. 478. Type locality, Goiás, Goiás, Brazil.

Vesperus melanopterus Jentink, 1904, p. 176. Type locality, Paramaribo, Surinam.

Eptesicus andinus J. A. Allen, 1914, p. 382. Type locality, Valle de las Papas, Huila, Colombia.

Eptesicus chiriquinus Thomas, 1920, p. 362. Type locality, Boquete, Chiriqui, Panama.

Eptesicus inca Thomas, 1920, p. 363. Type locality, Chanchamayo, Junín, Peru.

Eptesicus argentinus Thomas, 1920, p. 365. Type locality, Goya, Corrientes, Argentina.

Eptesicus brasiliensis thomasi Davis, 1966, p. 261. Type locality, Canelos, Napo-Pastaza, Ecuador.

Eptesicus brasiliensis (Demarest)—Besides the Huánuco and Junín records mentioned above, which I would refer to the species *E. brasiliensis*, Tuttle recorded this species from Loreto, Pasco, and Cajamarca. The specimens from Montealegre (AMNH 67232-33) are, however, not from the Department of Loreto. This locality is actually in Huánuco (see Vaurie, 1972), which adds that Department to the known records. The American Museum has no other Peruvian specimens. Unfortunately, the only altitudes given for either subspecies are *ca.* 270 m. (Nevati; San Juan) for the lowland subspecies (*thomasi*) and *ca.* 1250 m. (Vista Alegre, Rio Chinchao) and *ca.* 3600 m. (Maraynioc) for the highland ones (*andinus*). However, to judge from the coordinates given for all these localities by Vaurie (1972), the *b. thomasi* localities are all below and the *b. andinus* localities all above 1000 m. The highest locality (Maraynioc) is near timberline.

Eptesicus innoxius (Gervais)—Tuttle recorded this species only from Piura and Lambeyeque, both in the Pacific coastal region of northwestern Peru. The American Museum has no Peruvian specimens.

Eptesicus furinalis (D'Orbigny)—This is the species that Tuttle called *E. montosus*, following Davis (1966). The situation here is very similar to the problem with *andinus* and *brasiliensis*. The only constant difference is one of hair length with, again, the long-haired *montosus* occurring at higher elevations and the short-haired *furinalis* in the lowlands. On the same grounds, I regard the two subspecies of *montosus* to be referable to the species *E. furinalis*. As indicated above, I use *chiralensis* rather than *inca* as the name for the Peruvian

(highland) form. The formal synonymy would therefore stand:

Vespertilio furinalis D'Orbigny and Gervais, 1847, p. 13. Type locality, Corrientes, Argentina.

Adelonycteris gaumeri J. A. Allen, 1897b, p. 231. Type locality, Izamal, Yucatan, Mexico.

Eptesicus chapmani J. A. Allen, 1915, p. 632. Type locality, lower Rio Solimões, Amazonas, Brazil.

Eptesicus montosus Thomas, 1920, p. 363. Type locality, Chorro, Cochabamba, Bolivia.

Eptesicus chiralensis Anthony, 1926, p. 6. Type locality, El Chiral, El Oro, Ecuador.

Eptesicus gaumeri carteri Davis, 1965, p. 233. Type locality, Turrialba, Cartago, Costa Rica.

Eptesicus montosus is recorded by Tuttle only from two localities, both in Junín, one at *ca.* 900 m., the other at 1200 m., thus straddling the lower edge of the highlands of the Amazonian slopes. One might expect to find the Amazonian subspecies, *E. f. chapmani*, in the lowlands since it is known in Brazil, Colombia, and Bolivia, but if it does occur, it has not yet been recorded. The American Museum has no Peruvian specimens of this species except Tuttle's.

Histiotus macrotus (Poeppig)—Tuttle recorded this rare species from Puno and Huancavelica on the eastern slopes and from Arequipa on the Pacific side. No altitude is given for the Huancavelica record but it is certainly well above 3000 and probably closer to 4000 m. The record from Puno (Yanguyo) is stated by Pearson (1951) to be at *ca.* 3800 m., whereas the Arequipa one is probably below 1000 m. The American Museum has no specimens of this species, but Ceballos Bendezu (1955) recorded it from three localities in Cuzco, one of them stated to be at 3365 m.

Histiotis montanus (Philippi and Landbeck)—Tuttle recorded this rare bat from Cuzco and Puno and he gave as another locality "Hausampila," which is taken from Dobson (1878). According to Vaurie (1972), this is a variant spelling of "Huaisampillo" in Cuzco. The American Museum has no Peruvian specimens except for the type of *H. m. inambarus* (AMNH 37194) whose type locality is at *ca.* 700 m. Dobson's locality is stated to have an elevation of *ca.* 2750 m. If taken at face value, these two elevations span the known altitudinal

range in Peru and would seem to indicate occurrence in both lowlands and highlands of the eastern slopes. Unlike *H. macrotus* it is not known from the Pacific slope, and the highest elevation for *H. montanus* is considerably lower than any of the three eastern slope localities for *H. macrotus* for which altitudinal data are available.

Lasiurus borealis (Müller)—Tuttle recorded this species from Amazonas, Cuzco, and Puno on the eastern slopes and from Lima on the Pacific coast. The American Museum has no other specimens, but the Texas Cooperative Wildlife Collection has a specimen from Loreto. Altitudes on the Amazonian slopes range from the lowlands up to ca. 2150 m. The western localities are near sea level.

Lasiurus cinereus (Palisot de Beauvois)—Tuttle recorded this rare species only from Cuzco (2400 m.) Gardner (1976), however, also recorded it from Huánuco (ca. 3300 m.) and Ayacucho (1000 m.). The American Museum has no Peruvian specimens. The species in Peru seems confined to the highlands of the eastern slopes.

Lasiurus ega (Gervais)—Although Tuttle seemed uncertain about the occurrence of this species in Peru, it has been recorded (Handley, 1960; Gardner, 1976) from several localities, all in Loreto. In Peru it appears to be confined to the Amazonian lowlands.

Tomopeas ravus Miller—Tuttle recorded this Pacific coastal species from Piura, Lima, and Cajamarca. Davis (1970c), however, recorded it from Lambeyeque and, in addition, there is some uncertainty about the Department of one locality (Tulon) which Davis placed in Cajamarca, but Vaurie (1972) placed in La Libertad. The type locality in Cajamarca (Yayan, 1000 m.) is the highest known, but I have been unable to find precisely where it is. It may be Yayén (ca. lat. 6°30'S long., 78°15'N), but this town is at ca. 2700 m. It would be necessary to go ca. 10 km. east of Yayén before reaching 1000 m. In any case, the entire range of this isolated monotypic genus may be in the arid coastal portion of western Peru. However, if it occurs east of Yayén, this would put it into an isolated arid portion of the Amazon basin.

FAMILY MOLOSSIDAE

Molossops brachymeles (Peters)—Tuttle recorded this species only from an unknown locality in Peru, but Warner et al. (1974) recorded it (under the name of *M. abrasus*) from Loreto. The Texas Cooperative Wildlife Collection has a specimen from ca. 600 m. in Huánuco. The species is probably confined to the Amazonian lowlands.

Molossops planirostris (Peters)—This is the species called *milleri* by Tuttle, but this named form is still known only by the type from Loreto. After comparing the type (a subadult female) with adult females of *M. planirostris* from the state of Amazonas, Brazil, I can see no differences that cannot be explained by age and perhaps geographical variation, smaller size and darker coloration being the chief characters by which Osgood (1914) distinguished it from *M. planirostris*. I am therefore inclined to call *milleri* a subspecies (at best) of *M. planirostris*. The formal synonymy would therefore stand:

Molossus planirostris Peters, 1866b, p. 575. Type locality, Guyana.

Molossus planirostris paranus Thomas, 1901c, p. 190. Type locality, Pará, Brazil.

Molossops milleri Osgood, 1914, p. 183. Type locality, Yurimaguas, Loreto, Peru.

There are no other Peruvian records and this species would therefore appear to be confined to the Amazonian lowlands.

Molossops temmincki (Burmeister)—Tuttle recorded this species only from Pasco, but the American Museum has specimens from Loreto (Curaray River mouth, AMNH 71634-36). Both localities are in the Amazonian lowlands.

Tadarida brasiliensis (I. Geoffroy)—Tuttle recorded this species from San Martín, Cuzco, and Puno on the eastern slopes and from Lima and Arequipa on the Pacific side. Sanborn (1951) also recorded it from Huánuco and Ayacucho on the eastern side. The American Museum has no specimens other than the type and paratype of J. A. Allen's (1914) *peruana* from Puno. Tuttle indicated the highest known elevation as ca. 1850 m., but the Huánuco locality (near Ambo) is at ca. 2050 m. It reaches sea level on the Pacific side, but its

lowest known elevation on the eastern slopes is ca. 680 m. (Quincemil).

Tadarida macrotis (Gray)—Tuttle recorded this species only from Cuzco on the Amazonian side. The elevation of the single locality (Huajyumbe) is at ca. 630 m. The American Museum has no Peruvian specimens but the Texas Cooperative Wildlife Collection has specimens from Piura on the Pacific side.

Tadarida aurispinosa (Peale)—This is the species called *similis* by Tuttle. Carter and Davis (1961), however, showed that *similis* should be considered a subspecies of *T. aurispinosa*. The locality (Huajyumbe), the same as for *T. macrotis*, is in Cuzco, on the eastern slope at ca. 630 m. The American Museum has no Peruvian specimens, but de la Puente (1951) recorded it from Lima on the Pacific side. The Texas Cooperative Wildlife Collection has specimens from Piura, also on the Pacific side.

Tadarida laticaudata (E. Geoffroy)—Tuttle did not record this species, but the Texas Cooperative Wildlife Collection has a specimen from Piura on the Pacific side.

Tadarida (Mormopterus) kalinowskii (Thomas)—I follow Hill (1961) in considering *Mormopterus* a subgenus of *Tadarida*. Tuttle recorded this species from La Libertad and Lima on the Pacific slope and from Cajamarca (Hacienda Limón, not in Amazonas) in a restricted arid portion of the Amazon basin. The American Museum has no other specimens. All known localities are at less than 1000 m.

Tadarida (Mormopterus) phrudus Handley—This was recorded by Tuttle only from the original type material from Cuzco. The American Museum has a single specimen from the type locality (Machu Picchu, ca. 1850 m., AMNH 91553), which, except for lacking the anterior upper premolar on each side, agrees well with the original specimens. However, the species is still known only from the single locality in the highlands on the Amazonian slope.

Molossus ater E. Geoffroy—Tuttle recorded this species from San Martín, Huánuco, and Cuzco on the Amazonian slopes and questionably from Arequipa on the Pacific side. The American Museum has numerous specimens from Loreto (Boca Rio Curaray, AMNH 71396;

Lagarto, AMNH 78919; Puerto Indiana, AMNH 73976-83; Sarayacu, AMNH 75301-17) and a single one from Amazonas (Pomara, AMNH 69232). The Arequipa record is surely erroneous. Tuttle mentioned this department as a possibility since Tschudi (1844, p. 85) gave as the only locality where he obtained the species "an hacienda in the Ceja region 5000 feet above sea level on the eastern extension of the interior Cordillera" and the only locality Tuttle could find called Ceja is in Arequipa. However, it is clear from p. xxvii of the same work that Tschudi used the term "Ceja region" for an ecological zone on the eastern slope of the Andes. Arequipa and the Pacific slopes can therefore be deleted. The altitude of Tschudi's locality (ca. 1550 m.) is, however, considerably higher than the next highest known locality (Tingo Maria) at ca. 600 m. Aside from Tschudi's, all localities appear to be in the Amazonian lowlands.

Molossus molossus (Pallas)—Tuttle recorded this common widespread species from Loreto, Pasco, and Cuzco on the Amazonian side and from Piura and Lambayeque on the Pacific side. Warner et al. (1974) reported it from Huánuco and Ayacucho, while Osgood (1914) reported the species (under the name of *M. obscurus*) from San Martín. The American Museum has specimens from Amazonas (Cenipa River mouth, AMNH 98746, 98759-60, 98785) and Cajamarca (Jaen, AMNH 69234), both on the Amazonian side and the Field Museum has specimens from Junín (Huacapistana). Jaen, at ca. 2000 m., appears to be the highest record from which the species has been collected in the twentieth century, but Tuttle mentioned Dobson's (1878) record from ca. 2750 m. *Molossus molossus* would thus seem quite able to get across the relatively low passes of northern Peru. However, the populations of this species on the two sides of the Andes are quite distinct, the eastern slopes for the most part being inhabited by the large *M. m. crassicaudatus* and the western slopes by the small *M. m. daulensis*. However, *M. m. daulensis* is known from Huancabamba (Field Museum specimens), in Piura, in an isolated semi-arid portion of the Amazon basin.

Promops centralis Thomas—This is the species that Tuttle called *P. davisoni*, but I agree with Ojasti and Linares (1971) in regarding both *davisoni* and *occultus* as subspecies of *P. centralis*. Tuttle recorded this species only from Piura and Lima in the Pacific coastal region but the Field Museum has specimens from Lambayeque (Olmos). The American Museum has no Peruvian specimens, but the Texas Cooperative Wildlife Collection has specimens from ca. 600 m. in Huánuco. These belong to the quite distinct Amazonian lowland subspecies, *P. c. occultus*, rather than to *P. c. davisoni* of the Pacific side.

Eumops bonariensis (Peters)—Tuttle made no mention of this species but Eger (1977) recorded it from the Pacific side in Piura. The American Museum has no Peruvian specimens.

Eumops auripendulus (Shaw)—Tuttle recorded this species from Loreto, San Martín, Huánuco, and Junín on the Amazonian side and from Piura on the Pacific side. The American Museum has no other Peruvian specimens. Altitudes on the Amazonian slopes range from the lowlands to ca. 1250 m. (Vista Alegre in Huánuco).

Eumops glaucinus (Wagner)—Tuttle did not mention this species but Eger (1977) recorded it from Piura on the Pacific side. The American Museum has no Peruvian specimens.

Eumops perotis (Schinz)—As previously suggested (Koopman, 1971), I regard *trumbulli* as a subspecies of *E. perotis*. Eger (1977) considered them separate species because in her multivariate analyses "greater differences exist between *E. perotis* and *E. trumbulli* than between *E. auripendulus* and *E. underwoodi*" (which unlike *perotis* and *trumbulli* are sympatric). I have done no multivariate analysis but I have reexamined the skulls of all four species and come to somewhat different conclusions from those of Eger. I agree that there are two species pairs but see a greater difference between *underwoodi* and *auripendulus* than between *perotis* and *trumbulli*. Certainly the size difference is much greater in the former than in the latter. Another consideration is that *perotis* and *trumbulli* seem more highly derived than *underwoodi* and *auripendulus* and therefore

their special resemblances are probably more significant than those of *underwoodi* and *auripendulus*, which may be, at least in part, only retained primitive characters. Eger (1977, p. 58) also mentioned the greater reduction of the last upper molar in *E. perotis* than in *E. trumbulli*. However, I find considerable variation in this character, but no consistent difference between the two alleged species. I find, for instance, little difference in the size of the last upper molar between AMNH 15751 (*p. californicus* from California) and AMNH 209902 (*trumbulli* from Bolivia). The formal synonymy would therefore stand:

Molossus perotis Schinz, 1821, p. 870. Type locality, Villa São Salvador, Campos dos Goitacazes, Rio Paraíba, Rio de Janeiro, Brazil.

Dysopes (Molossus) gigas Peters, 1865, p. 381. Type locality, Cayajabos, Mariel, Pinar del Rio, Cuba.

Molossus californicus Merriam, 1890, p. 31. Type locality, Alhambra, Los Angeles co., California, United States.

Promops trumbulli Thomas, 1901a, p. 190. Type locality, Pará, Brazil.

Eumops perotis renatae Pirlot, 1965, p. 5. Type locality, Cumaná, Sucre, Venezuela.

Tuttle recorded this species from Loreto and San Martín on the Amazonian slopes and from Lima on the Pacific side. Eger (1977) also recorded this species from Huancavelica on the Pacific side. The altitude of the last locality (Cordova) is not given but is at ca. 3000 m. The American Museum has no Peruvian specimens. All the specimens I have seen from the Amazonian slopes are referable to the smaller *E. p. trumbulli*, whereas those from the Pacific side are *E. p. perotis*. In the Amazonian drainage, the species clearly occurs in the lowlands, but its maximum altitudinal limits are not clear since I do not know the altitude of one of the San Martín localities (Rumispa). The other two (Juan Guerra and the Rio Ponasa) are both under 500 m.

[*Eumops trumbulli* (Thomas)]—As indicated above, I believe that *trumbulli* is only a subspecies of *E. perotis*. As previously pointed out (Koopman, 1971), Sanborn's (1932) Loreto record of *E. p. perotis* actually pertains to *E. p. trumbulli*.

DISCUSSION

A number of people have undertaken ecological analyses of Peru and neighboring regions, at least since the days of Tschudi (1844). The problem of delimiting zones and regions is a complex one. The Peruvian Andes are a formidable barrier (particularly in the south) to faunal dispersal between the Amazon basin and the Pacific coast. In addition, except in the extreme north, the presence of the Andes causes an extreme difference in moisture between its two sides, the wet Amazon basin and the dry Pacific coast. Furthermore, since the Andes do not form a single ridge, the upper reaches of the Rio Marañon and (to a lesser extent) the Rio Huallaga, while part of the Amazon drainage, are cut off from the rain of the main Amazon basin and are therefore ecologically more similar to the arid Pacific coast. At the extreme northwestern corner of Peru, the coastal region receives markedly more rain than does the coast farther south (see Chapman, 1926, for details). This wetter strip extends somewhat farther south with higher altitude on the Pacific slopes of the Andes so that even its most mesic expression, the Colombian-Pacific Fauna of Chapman, does barely get into Peru (particularly at Palambla in Piura). Since this mesic area of extreme northwestern Peru is close to the relatively low trans-Andean passes, derivation of its faunal elements from either the north or the east is possible even though, at least at present, the passes themselves are quite dry. These relationships are shown in table 3.

The mesic eastern slopes of the Andes exhibit a great deal of diversity from the Amazonian lowlands to timberline and above. This gradient has been divided in various ways (see fig. 1). At least part of the disagreement reflects local differences in rainfall, soils, slope, and other factors. Chapman (1926) recognized a Tropical Zone ranging from sea level up to from 1350 to 1850 m., a Subtropical Zone from there to 2750-2900 m., a Temperate Zone from there to 3300-4000 m. and finally a Paramo Zone (above timberline) on up to 4500 m. Hammen (1974) recognized a Lower tropical forest (up to 1000 m.), Subandean forest

(1000-2500 m.), Andean forest (2500-3500 m.), Subparamo (3500-3800 m.), and Paramo (3800-4200 m.). Both these authors were dealing with areas to the north (Ecuador and Colombia, respectively.) In contrast, Terborgh (1971) working in a very limited area in Peru (west side of Cordillera Vilcabamba in Cuzco), from which many bats used in this study were collected, had still another breakdown. He recognized Lowland rainforest (up to 650 m.), Montane rainforest (650-1380 m.), Cloud forest (1380-2550 m.), and "Monte chico" (2550-3500 m.). The two rainforest zones of Terborgh correspond roughly with the Tropical Zone of Chapman. The Cloud Forest of Terborgh, the Subandean Forest of Hammen, and the Subtropical Zone of Chapman are roughly comparable; likewise the Monte chico of Terborgh roughly corresponds to the Andean forest of Hammen and the Temperate Zone of Chapman. Terborgh and Weske (1975) presented a somewhat different zonation for a limited area in Huánuco, from which many of the bats used in this study were collected. In tables 1 and 2, I have tried to indicate several critical altitudinal levels (650 m., 1000 m., 1400 m., 2500 m.). Nevertheless, my basic division into highland (table 2) and lowland (table 1) has been set, perhaps arbitrarily, at 1000 m. The three tables include all but three of the species of bats known from Peru. These species (*Centronycteris maximiliani*, *Diclidurus scutatus*, *Micronycteris behni*) are too poorly known in Peru for anything useful to be said about their distributional pattern in that country. It should be emphasized that for many other species, the distributional picture is obviously incomplete. A few cases, where the probability is great that a species occurs in a certain area or zone but there are no records to support this, are indicated by question marks. The Peruvian bat fauna is very large (ca. 122 species) but still rather poorly known, as Tuttle (1970) pointed out. Approximately one-seventh of the total number of species of bats in the world and two-thirds of those in South America are now known from Peru, but our knowledge of their distribution, as with most other aspects of their biology, is very incomplete and is certainly

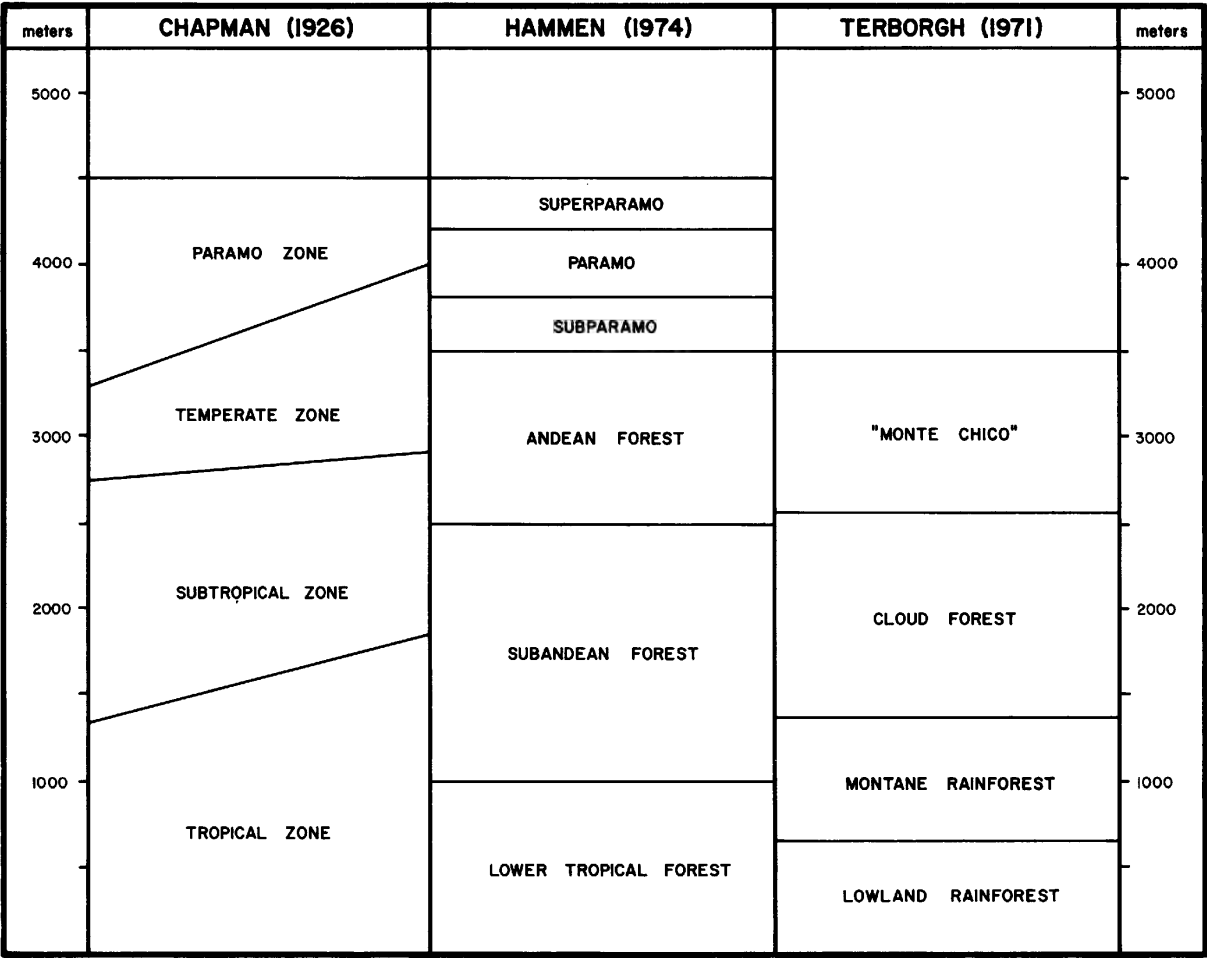


FIG. 1. Three attempts to partition the altitudinal gradient on the eastern slope of the Andes in Colombia, Ecuador, and Peru.

crude by avian standards. However, I think the analysis can be carried considerably beyond Tuttle's (1970) presentation. The sections to follow can be considered extended commentaries on the three tables.

Amazonian Lowland Species (table 1.). This is the largest group (99 species). Six species (marked *) *Vampyrops dorsalis*, *Artibeus harti*, *Myotis oxyotus*, *Eptesicus furinalis*, *Histiotus montanus*, and *Tadarida brasiliensis* are basically highland forms but are included because they are known to occur below 1000 m. (but not below 650 m.). The others are all Amazonian lowland by any standards. Probably there are a number of others which will be found in the Amazonian lowlands of Peru, since about 20 additional species are known from adjacent

parts of the Amazonian lowlands. Of the species listed in table 1, 63 species extend above 650 m. and 45 species extend above 1000 m. and are therefore here considered to be also highland species. Again, there are probably other species that also do so but have not yet been recorded.

Amazonian Highland Species (table 2). Fifty-five species are listed of which 50 extend below 1400 m. (into the Tropical Zone of Chapman) and 45 below 1000 m. and therefore occur definitely in the lowlands. On the other hand, 22 extend above 1500 m. (into the Andean forest of van der Hammen or the Monte Chico of Terborgh). Only 20 species (*Vampyrops infuscus* a possible addition) reach the Pacific slopes, 10 of these not being known

TABLE 1
Altitudinal Distribution of Mesic Amazonian Lowland Species

Mesic Amazonian Lowland Species	Above 650 m.	Above 1000 m.	Mesic Amazonian Lowland Species	Above 650 m.	Above 1000 m.
<i>Rhynchonycteris naso</i>	—	—	<i>Sturnira tildae</i>	—	—
<i>Saccopteryx bilineata</i>	+	—	<i>Uroderma bilobatum</i>	+	+
<i>Saccopteryx canescens</i>	—	—	<i>Uroderma magnirostrum</i>	—	—
<i>Saccopteryx leptura</i>	+	—	<i>Vampyrops dorsalis*</i>	+	+
<i>Cormura brevirostris</i>	+	—	<i>Vampyrops lineatus</i>	+	+
<i>Peropteryx kappleri</i>	+	+	<i>Vampyrops infuscus</i>	+	+
<i>Peropteryx macrotis</i>	+	+	<i>Vampyrops helleri</i>	+	—
<i>Peropteryx leucopterus</i>	—	—	<i>Vampyrops brachycephalus</i>	+	—
<i>Diclidurus albus</i>	—	—	<i>Vampyrodes caracciolo</i>	+	—
<i>Noctilio albiventris</i>	—	—	<i>Vampyressa bidens</i>	+	—
<i>Noctilio leporinus</i>	—	—	<i>Vampyressa pusilla</i>	+	+
<i>Pteronotus parnellii</i>	+	—	<i>Chiroderma trinitatum</i>	+	—
<i>Pteronotus gymnotus</i>	+	+	<i>Chiroderma villosum</i>	+	—
<i>Micronycteris hirsuta</i>	—	—	<i>Ectophylla macconnelli</i>	+	+
<i>Micronycteris megalotis</i>	+	+	<i>Artibeus harti*</i>	+	+
<i>Micronycteris minuta</i>	—	—	<i>Artibeus cinereus</i>	+	+
<i>Micronycteris nicefori</i>	—	—	<i>Artibeus anderseni</i>	+	—
<i>Micronycteris sylvestris</i>	+	—	<i>Artibeus concolor</i>	—	—
<i>Micronycteris daviesi</i>	—	—	<i>Artibeus fuliginosus</i>	+	+
<i>Lonchorhina aurita</i>	+	—	<i>Artibeus planirostris</i>	+	+
<i>Macrophyllum macrophyllum</i>	—	—	<i>Artibeus lituratus</i>	+	+
<i>Tonatia brasiliensis</i>	—	—	<i>Sphaeronycteris toxophyllum</i>	—	—
<i>Tonatia carrikeri</i>	—	—	<i>Desmodus rotundus</i>	+	+
<i>Tonatia bidens</i>	—	—	<i>Desmodus youngi</i>	—	—
<i>Tonatia sylvicola</i>	+	+	<i>Diphylla ecaudata</i>	+	+
<i>Mimon crenulatum</i>	+	+	<i>Furipterus horrens</i>	—	—
<i>Phyllostomus discolor</i>	+	—	<i>Thyroptera discifera</i>	—	—
<i>Phyllostomus elongatus</i>	+	+	<i>Thyroptera tricolor</i>	+	+
<i>Phyllostomus hastatus</i>	+	+	<i>Myotis nigricans</i>	+	+
<i>Phylloderma stenops</i>	+	+	<i>Myotis albescens</i>	+	+
<i>Trachops cirrhosus</i>	—	—	<i>Myotis simus</i>	—	—
<i>Vampyrus spectrum</i>	—	—	<i>Myotis riparius</i>	+	—
<i>Glossophaga soricina</i>	+	+	<i>Myotis oxyotus*</i>	+	+
<i>Lonchophylla thomasi</i>	—	—	<i>Eptesicus brasiliensis</i>	+	+
<i>Lonchophylla robusta</i>	+	—	<i>Eptesicus furinalis*</i>	+	+
<i>Lionycteris spurrelli</i>	+	+	<i>Histiotus montanus*</i>	+	+
<i>Anoura brevirostrum</i>	+	+	<i>Lasiurus borealis</i>	+	+
<i>Anoura caudifer</i>	+	+	<i>Lasiurus ega</i>	—	—
<i>Anoura geoffroyi</i>	+	+	<i>Molossops brachymeles</i>	—	—
<i>Choeroniscus intermedius</i>	—	—	<i>Molossops planirostris</i>	—	—
<i>Choeroniscus minor</i>	—	—	<i>Molossops temmincki</i>	—	—
<i>Lichonycteris obscura</i>	—	—	<i>Tadarida brasiliensis*</i>	+	+
<i>Carollia castanea</i>	+	+	<i>Tadarida macrotis</i>	—	—
<i>Carollia perspicillata</i>	+	+	<i>Tadarida aurispinosa</i>	—	—
<i>Carollia brevicauda</i>	+	+	<i>Molossus ater</i>	+	+
<i>Rhinophylla pumilio</i>	+	—	<i>Molossus molossus</i>	+	+
<i>Rhinophylla fischeri</i>	+	—	<i>Promops centralis</i>	—	—
<i>Sturnira lilium</i>	+	+	<i>Eumops auripendulus</i>	+	+
<i>Sturnira ludovici</i>	+	+	<i>Eumops perotis</i>	—	—
<i>Sturnira magna</i>	+	+			

TABLE 2
Distribution of Amazonian Highland Species

Amazonian Highland Species	Below 1000 m.	Below 1400 m.	Above 2500 m.	Pacific Slope
<i>Peropteryx kappleri</i>	+	+	—	—
<i>Peropteryx macrotis</i>	+	+	—	—
<i>Pteronotus davyi</i>	—	—	—	+
<i>Pteronotus gymnonotus</i>	+	+	—	—
<i>Micronycteris megalotis</i>	+	+	+	+
<i>Tonatia sylvicola</i>	+	+	—	+
<i>Mimon crenulatum</i>	+	+	—	—
<i>Phyllostomus elongatus</i>	+	+	—	—
<i>Phyllostomus hastatus</i>	+	+	—	+
<i>Phylloderma stenops</i>	+	+	+	+
<i>Glossophaga soricina</i>	+	+	—	+
<i>Lionycteris spurrelli</i>	+	+	—	—
<i>Anoura brevirostrum</i>	+	+	—	—
<i>Anoura caudifer</i>	+	+	+	—
<i>Anoura geoffroyi</i>	+	+	+	+
<i>Carollia castanea</i>	+	+	—	—
<i>Carollia perspicillata</i>	+	+	—	+
<i>Carollia brevicauda</i>	+	+	—	—
<i>Sturnira bidens</i>	—	—	+	—
<i>Sturnira nana</i>	—	—	—	—
<i>Sturnira erythromos</i>	—	+	+	—
<i>Sturnira lilium</i>	+	+	—	+
<i>Sturnira ludovici</i>	+	+	+	—
<i>Sturnira magna</i>	+	+	—	—
<i>Uroderma bilobatum</i>	+	+	—	+
<i>Vampyrops dorsalis</i>	+	+	+	—
<i>Vampyrops lineatus</i>	+	+	+	—
<i>Vampyrops infuscus</i>	+	+	—	?
<i>Vampyrops vittatus</i>	—	+	+	—
<i>Vampyressa melissa</i>	—	+	—	—
<i>Vampyressa pusilla</i>	+	+	—	—
<i>Ectophylla macconnelli</i>	+	+	—	—
<i>Artibeus harti</i>	+	+	+	—
<i>Artibeus cinereus</i>	+	+	+	—
<i>Artibeus fuliginosus</i>	+	+	—	—
<i>Artibeus planirostris</i>	+	+	—	—
<i>Artibeus lituratus</i>	+	+	—	—
<i>Desmodus rotundus</i>	+	+	+	+
<i>Diphylla ecaudata</i>	+	+	—	—
<i>Thyroptera tricolor</i>	+	+	—	—
<i>Myotis nigricans</i>	+	+	+	+
<i>Myotis keaysi</i>	—	+	+	+
<i>Myotis albescens</i>	+	+	—	+
<i>Myotis oxyotus</i>	+	+	+	+
<i>Eptesicus brasiliensis</i>	+	+	+	—
<i>Myotis furinalis</i>	+	+	—	—
<i>Histiotus macrotus</i>	—	—	+	+
<i>Histiotus montanus</i>	+	+	+	—

TABLE 2 — (Continued)

Amazonian Highland Species	Below 1000 m.	Below 1400 m	Above 2500 m.	Pacific Slope
<i>Lasiurus borealis</i>	+	+	—	+
<i>Lasiurus cinereus</i>	—	+	+	—
<i>Tadarida brasiliensis</i>	+	+	—	+
<i>Tadarida phrudus</i>	—	—	—	—
<i>Molossus ater</i>	+	+	—	—
<i>Molossus molossus</i>	+	+	+	+
<i>Eumops auripendulus</i>	+	+	—	+

from the Amazonian highlands above 2500 m. The significance of this phenomenon will be discussed below.

Pacific Slope Species (table 3). I have indicated for each of the 40 species whether they occur in the more mesic area of northwestern Peru (parts of Tumbes, Piura, and the north-eastern edge of Lambayeque, or the more arid Pacific slope farther south and nearer the coast. I have also indicated which species are known to reach the arid interior valleys of the Amazon basin and which reach the more mesic main Amazonian drainage. A few uncertainties are indicated by question marks. The 29 species I have listed as mesic Pacific are probably somewhat less than the true figure inasmuch as the American Museum has specimens of nine additional species from the Pacific slopes of southwestern Ecuador (provinces of Guayas, El Oro, Azuay, and Loja). Several of these probably reach northwestern Peru. Nineteen species are known from the arid Pacific slopes of Peru, of which 11 definitely occur in the arid interior valleys. The number of the latter is, however, probably greater since the bats from these valleys are poorly known. On the Pacific slopes, conditions become steadily drier the farther south one goes, and this is reflected in the decreasing number of bat species. Twenty-three species are not known to occur south of Lambayeque, one more not south of Libertad, six more not south of Lima, one more not south of Ica and the adjoining part of Huancavelica, two more not south of Arequipa. However, six species do reach Chile, although there may well be gaps in the ranges. Twenty-eight species listed in table 3 are definitely known from the main mesic portion of the Amazon basin, though

Histiotus macrotus is not known to occur below 3000 m. on the Amazonian side.

Ecological Replacement Among Peruvian Bats—It should be clear from the previous sections that our understanding of geographical and ecological distribution of Peruvian bats is still woefully incomplete and therefore any generalizations must be very crude. However, for a few genera, particularly ones for which Weske and Terborgh collected numerous specimens from various altitudes, some definite patterns emerge. In some cases, interesting relationships are found on the two sides of the Andes. *Mimon crenulatum* is represented by two very distinct Amazonian lowland subspecies, *M. c. longifolium* and the highland *M. c. koepckeeae*, which Gardner and Patton (1972) considered separate species. *Glossophaga soricina* is represented by the mesic Amazonian subspecies, *G. s. soricina* and by a different subspecies, *G. s. valens*, which occurs both on the Pacific slopes and in the arid Amazonian interior valleys. *Lonchophylla hesperia* of the Pacific coast could be said to represent *L. robusta* of the Amazon basin, but the relationship is not close. In *Sturnira*, there are two instances of altitudinal replacement. The small lowland *S. lilium* is replaced at approximately 1200 m. by the small highland *S. erythromos*. The larger lowland *S. tildae* (at elevations less than 650 m.) is replaced (though with some overlap) by the chiefly highland *S. ludovici* (similar to *tildae* in size). It might be mentioned that though *ludovici* does reach quite low elevations in central Peru, it is not known from Loreto nor does it extend across the Amazon basin to eastern South America as *tildae* does. The genus *Vampyrops* also exhibits an apparent case of re-

TABLE 3
Distribution of Pacific Slope Species

Pacific Slope Species	Arid Pacific	Arid Amazonian	Mesic Pacific	Mesic Amazonian
<i>Saccopteryx bilineata</i>	—	—	+	+
<i>Noctilio leporinus</i>	—	—	+	+
<i>Pteronotus davyi</i>	—	—	+	+
<i>Micronycteris megalotis</i>	—	—	+	+
<i>Tonatia sylvicola</i>	—	—	+	+
<i>Phyllostomus discolor</i>	—	—	+	+
<i>Phyllostomus hastatus</i>	—	—	+	+
<i>Phylloderma stenops</i>	—	—	+	+
<i>Glossophaga soricina</i>	+	+	+	+
<i>Lonchophylla hesperia</i>	+	+	—	—
<i>Platalina genovensium</i>	+	+	—	—
<i>Anoura geoffroyi</i>	+	+	+	+
<i>Carollia perspicillata</i>	—	—	+	+
<i>Sturnira lilium</i>	—	—	+	+
<i>Uroderma bilobatum</i>	—	—	+	+
<i>Vampyrops helleri</i>	—	—	+	+
<i>Artibeus fraterculus</i>	+	+	+	—
<i>Artibeus lituratus</i>	—	—	+	+
<i>Desmodus rotundus</i>	+	+	+	+
<i>Amorphochilus schnablii</i>	+	+	—	—
<i>Myotis nigricans</i>	—	—	+	+
<i>Myotis atacamensis</i>	+	—	—	—
<i>Myotis keaysi</i>	—	—	+	+
<i>Myotis albescens</i>	—	—	+	+
<i>Myotis oxyotus</i>	+	+	—	+
<i>Eptesicus innoxius</i>	+	—	+	—
<i>Histiotus macrotis</i>	+	—	—	—
<i>Lasiurus borealis</i>	+	+	—	+
<i>Tomopeas rarus</i>	+	?	—	—
<i>Tadarida brasiliensis</i>	+	—	—	+
<i>Tadarida macrotis</i>	—	—	+	+
<i>Tadarida aurispinosa</i>	+	—	+	+
<i>Tadarida laticaudata</i>	—	—	+	—
<i>Tadarida kalinowskii</i>	+	+	—	—
<i>Molossus molossus</i>	+	+	+	+
<i>Promops centralis</i>	+	—	+	+
<i>Eumops bonariensis</i>	—	—	+	—
<i>Eumops auripendulus</i>	—	—	+	+
<i>Eumops glaucinus</i>	—	—	+	—
<i>Eumops perotis</i>	+	—	—	+

placement. The large mainly lowland *V. infuscus* (though it does reach approximately 1500 m., the upper edge of the Tropical Zone of Chapman and the Montane rainforest of Terborgh) is replaced by the large highland *V. vittatus*. There is, however, some overlap since *vittatus* extends down to approximately 1000 m.

The small lowland *V. helleri* is represented by distinctive subspecies on the two sides of the Andes, *V. h. incarum* on the Amazonian side and *V. h. helleri* on the Pacific side. In *Vampyressa*, the Amazonian highland *V. melissa* may be said to represent the Amazonian lowland *V. pusilla* but the species are quite dis-

tinct. In *Ectophylla macconnelli*, Amazonian lowland populations are referable to *E. m. macconnelli* but Amazonian highland populations are referable to *E. m. flavescens*. In *Artibeus cinereus* there is also altitudinal differentiation, the lowland populations below 650 m. being referable to *A. c. pumilio*, those from above 650 m. to the rather distinct *A. c. glaucus*. Patten (1971) believed that *A. fuliginosus* of the Amazon basin is represented by *A. fraterculus* of the Pacific coast and some dry interior valleys but this seems unlikely to me, based on comparison of the two forms. The populations of *Amorphochilus schnablii* from the coast and interior valleys have been put into different subspecies (*A. s. schnablii* and *A. s. osgoodi*, respectively), but the differences are slight. In *Myotis nigricans*, the Amazonian (*M. n. caucensis*) and Mesic Pacific (*M. n. punensis*) representatives are distinct, and a closely related species (*M. atacamensis*) occurs in the arid Pacific zone. Another related species (*M. keaysi*) may be said to represent *M. nigricans* in the highlands, though with considerable overlap. There are also interesting relationships in *Eptesicus*. In Amazonian Peru, *E. brasiliensis* is represented by *E. b. thomasi* in the lowlands and by the very distinct *E. b. andinus* in the highlands. *Eptesicus innoxius* of the Pacific slopes probably represents *E. furinalis* of the Amazon basin. *Histiotus macrotus* of the Pacific slope and the highlands of the eastern slopes above 2800 m. seems to represent *H. montanus* at lower elevations on the Amazonian slopes. This altitudinal separation would correspond to the division between the Temperate Zone and Subtropical Zone of Chapman. *Tadarida kalinowskii* of the Pacific coast and arid Amazonian valleys and *T. phrudus* of the highlands of the eastern slopes might be considered representatives, but the relationship is not very close. *Molossus molossus* is represented by two quite different subspecies in Peru. The Amazonian lowlands and highlands are occupied by the large *M. m. crassicaudatus*, whereas the small *M. m. daulensis* occurs on the Pacific slopes. *Promops centralis* is represented by quite different subspecies on the Amazonian (*P. c. occultus*) and Pacific (*P. c. davisoni*) sides, which until recently were regarded as separate species. Finally, *Eumops perotis* is an-

other species with very distinct subspecies on the Pacific slope (*E. p. perotis*) and in the Amazonian lowlands (*E. p. trumbulli*).

Geographical Affinities of the Mesic Pacific Species. The affinities of the populations of the 29 species present a problem. On one hand, they are in ecological contact with Ecuadorian populations and could have come from the north. As indicated above, there are several additional western Ecuadorian species that may enter extreme northwestern Peru. On the other hand, this northwestern corner of Peru is adjacent to the relatively low passes across the Andes and these provide an alternate means of entry. Of the species of the small mesic portion of northwestern Peru, only nine (*Pteronotus davyi*, *Micronycteris megalotis*, *Tonatia sylvicola*, *Phyllostomus hastatus*, *Phylloderma stenops*, *Vampyrops helleri*, *Tadarida aurispinosa*, *T. laticaudata*, *Eumops bonariensis*) are not known from western Ecuador to my knowledge. With the exception of *Tadarida laticaudata* and *Eumops bonariensis*, all of these occur on the Amazonian side of Peru, though in the case of *Vampyrops helleri* the subspecies are different, the Pacific population belonging to the Central American subspecies (*V. h. helleri*), which has presumably come in from the north, though there are no Ecuadorian records. Entry from the north is also made more probable by the absence of *V. helleri* from the highlands of the Amazonian slope. The six remaining species (*Pteronotus davyi*, *Micronycteris megalotis*, *Tonatia sylvicola*, *Phyllostomus hastatus*, *Phylloderma stenops*, *Tadarida aurispinosa*) are the most likely candidates for entry through the northern Peruvian passes. For most of the species that do occur in western Ecuador, derivation from there seems to me more likely than from across the Andes, since the Andean passes would in most cases have had to have been both warmer and wetter to allow passage. For *Molossus molossus*, northern entry is certainly more probable since the Pacific subspecies (*M. m. daulensis*) more closely resembles the southern Central American *M. m. coibensis* than the Amazonian *M. m. crassicaudatus*. For *Eumops glaucinus* northern entry is more probable since the species is not known from the eastern slopes of Peru. This may, however, be an artifact of lack of collect-

ing. For the remaining species, there is little basis for choice, but I suspect that in the immediate past, the Andean passes have only been available to arid-tolerant species.

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